THE

AMERICAN NATURALIST

VOL. XLV | July, 1911 | NO. 535

GERM-CELL DETERMINANTS AND THEIR SIGNIFICANCE[1]

PROFESSOR R. W. HEGNER

UNIVERSITY OF MICHIGAN

INVESTIGATIONS of the origin of the germ cells in a number of animals have brought forth certain phenomena which indicate that these cells are determined as such at a very early period in embryonic development, and that in some cases the material which apparently determines the germ cells is visible at this time. Conclusions can be drawn from these observations which are of considerable interest.

The frequently repeated statement that the germ cells are derived from the mesoderm or from the entoderm is of course erroneous in those instances where the germ cells can be identified before the formation of the germ layers, and it seems probable that the primary cell differentiation, *i. e.*, the separation of the germ cells from the somatic cells, takes place at an early period in the embryonic development of even those animals where this has not been actually observed. A few of the most pronounced cases of the early differentiation of germ cells are briefly described in the following paragraphs and several general conclusions arrived at from this evidence.

The best known example is *Ascaris*, as described by

[1] Contributions from the Zoological Laboratory of the University of Michigan, No. 135. From a paper read before the Research Club of the University of Michigan, November 9, 1910.

Boveri ('92). The first cleavage division of the egg of *Ascaris* results in two daughter cells, each containing two long chromosomes (Fig. 1, *A*). In the second division the chromosomes of one cell divide normally and each daughter cell receives one half of each (Fig. 1, *B, s*). The chromosomes of the other cell behave differently; the thin middle portion of each breaks up into granules

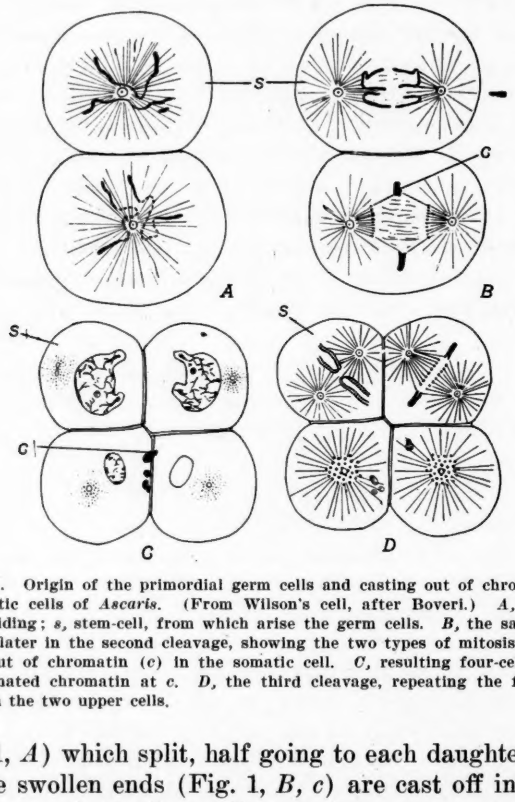

FIG. 1. Origin of the primordial germ cells and casting out of chromatin in the somatic cells of *Ascaris*. (From Wilson's cell, after Boveri.) *A*, two-cell stage dividing; *s*, stem-cell, from which arise the germ cells. *B*, the same from the side, later in the second cleavage, showing the two types of mitosis and the casting out of chromatin (*c*) in the somatic cell. *C*, resulting four-cell stage; the eliminated chromatin at *c*. *D*, the third cleavage, repeating the foregoing process in the two upper cells.

(Fig. 1, *A*) which split, half going to each daughter cell, but the swollen ends (Fig. 1, *B, c*) are cast off into the cytoplasm. In the four-cell stage there are consequently two cells with the full amount of chromatin and two with a reduced amount. This inequality in the amount of chromatin results in different sized nuclei (Fig. 1, *C*); those with entire chromosomes (*s*) are larger than those that have lost the swollen ends (*c*). In the third division

one of the two cells with the two entire chromosomes loses the swollen ends of each; the other (Fig. 1, *D*, *s*) retains its chromosomes intact. A similar reduction in the amount of chromatin takes place in the fourth and fifth divisions and then ceases. The single cell in the thirty-two-cell stage which contains the full amount of chromatin has a larger nucleus than the other thirty-one cells and gives rise to all of the germ cell, whereas the other cells are for the production of somatic cells only.

The primordial germ cell of *Ascaris*, therefore, contains two entire chromosomes; every other cell possesses two chromosomes which have lost part of their substance. In other words, the germ cells possess a certain amount of chromatic material not present in the somatic cells.

There is also an early differentiation of the germ cells in the fresh water crustacean, *Cyclops* (Haecker, '97). According to Haecker, "Aussenkörnchen" arise at one pole of the first cleavage spindle (Fig. 2, *A*, *ak*); these

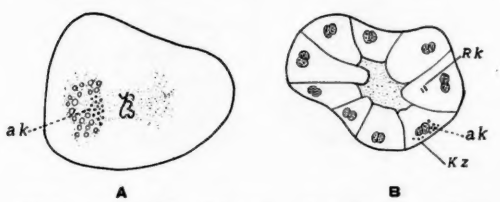

FIG. 2. Origin of the primordial germ cell in *Cyclops*. (From Haecker.) *A*, the first cleavage division, showing the "Aussenkörnchen" (*ak*) at one pole of the spindle. *B*, the thirty-two-cell stage; the primordial germ cell (*Kz*) contains all of the "Aussenkörnchen" (*ak*).

are derived from disintegrated nucleolar material and are attracted to one pole of the spindle by a dissimilar influence of the centrosomes. During the first four cleavage divisions the granules are segregated always in one cell (Fig. 2, *B*, *kg*); at the end of the fourth division these "Aussenkörnchen" disappear, but the cell which contained them can be traced by its delayed mitotic phase and is shown to be the primordial germ cell.

In this case, as in that of *Ascaris*, the primordial germ cell and the germ cells derived from it possess certain nuclear materials not present in the somatic cells. The

latter seem to be limited because of their absence to the performance of vegetative functions, and the germ cells appear to have the power of reproduction because of their presence.

A recent paper by Elpatiewsky (1909) deals with the early embryonic development of the arrow worm, *Sagitta.* This investigator finds that, at the stage when the two pronuclei are in the center of the egg, a body appears at the vegetative pole lying near the periphery (Fig. 3,

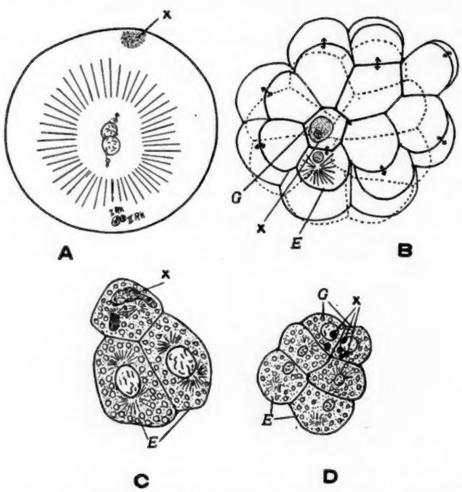

FIG. 3. Origin of the primordial germ cells in *Sagitta.* (From Elpatiewsky.) *A,* egg with conjugating pronuclei; polar bodies (*I Rk.* and *II Rk.*) and "besonderer körper" (x) embedded in cytoplasm. *B,* thirty-two-cell stage; the primordial germ cell (G) contains the "besonderer körper" (x); entoderm cell at E. *C,* the primordial germ cell dividing; the "besonderer körper" (x) within it is also dividing; the entoderm cell has already divided (E). *D,* two germ cells (G) resulting from the first division of the primordial germ cell; each contains part of the "besonderer körper" (x).

A). This body, which is termed "besondere körper," consists of coarse granules which do not stain quite so deeply as the chromosomes. During the first four cleavage divisions the "besondere körper" does not divide, but is always to be found in one blastomere. In the fourth division the blastomere which contains this body divides unequally; the larger cell is destined to produce the entoderm (Fig. 3, *B, E*); the smaller cell, which con-

tains the "besondere körper" is the primordial germ cell (Fig. 3, *B, G*). The first division of this primordial germ cell (Fig. 3, *C*) results in two daughter cells, one of which obtains a larger portion of the "besondere körper" (*X*) than the other (Fig. 3, *D*). This is interpreted as the differential division, the cell which possesses the larger amount of the divided "besondere körper" giving rise to the male germ cells, the other to the female germ cells in the hermaphroditic adult. The "besondere körper" now gradually becomes paler and finally disappears. Buchner ('10) and Stevens ('10) have confirmed Elpatiewsky's observations. The origin of the "besondere körper" was not determined.

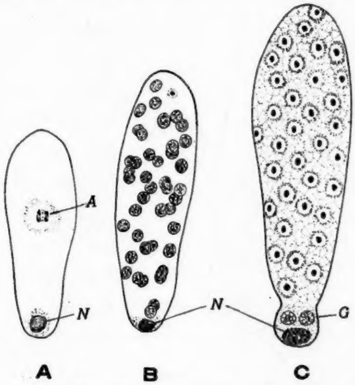

FIG. 4. Origin of the primordial germ cells of *Oophthora*. (From Silvestri.) *A*, the nucleolus (*N*) of the germinal vesicle (*A*) has passed to the posterior end of the egg. *B*, an egg containing a number of cleavage nuclei. *C*, the cells which come under the influence of the nucleolus (*N*) become the primordial germ cells (*G*).

These investigations show the germ cells of *Sagitta* to be similar to those of *Ascaris* and *Cyclops* in that they contain a darkly staining material not present in the somatic cells.

In *Oophthora* and other parasitic hymenoptera, Sylvestri ('09) finds that the nucleolus of the germinal vesicle passes to the posterior end of the egg during maturation (Fig. 4, *A*). Here it remains until the cleavage nuclei reach the periphery (Fig. 4, *B*). The cells which then come under the influence of the nucleolus be-

come the primordial germ cells (Fig. 4, *C, G*) and give rise to the germ glands of the adult. The similarity between this process and that described for *Ascaris, Cyclops* and *Sagitta* is obvious.

Finally in chrysomelid beetles the primordial germ cells are differentiated at a very early period (Hegner, '09). At the posterior end of the eggs of *Calligrapha multipunctata* and allied species there is a disc-shaped mass of granules which stain like chromatin. I have called this the pole disc (Fig. 5, *A, gc. d*). When the cleavage nuclei reach the periphery of the egg they fuse with the superficial layer of cytoplasm everywhere except at the posterior end; cell walls then appear and a blastoderm is formed. When the cleavage nuclei which reach the posterior end of the egg encounter the pole disc granules they gather these granules about them and continue their migration (Fig. 5, *B, gc*); cell walls are formed, and they finally come to lie entirely outside of the egg (Fig. 5, *C, gc*).

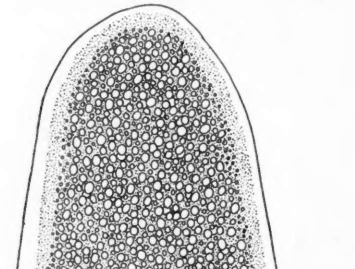

FIG. 5.

There are sixteen cells which separate from the egg in this manner, and they take out of the egg with them practically all of the pole disc granules (Fig. 5, *C, pd.g*). These sixteen cells divide to form thirty-two; in this division apparently one half of the granules contained in each cell pass to each of the daughter cells (Fig.

5, *D*, *pd.g*). A second division results in sixty-four cells; this number is constant until a late stage in embryonic development.

These sixty-four cells have been traced through the early embryonic stages. First they migrate back into the egg through a "pole cell canal" (Fig. 5, *C*, *pc*) sit-

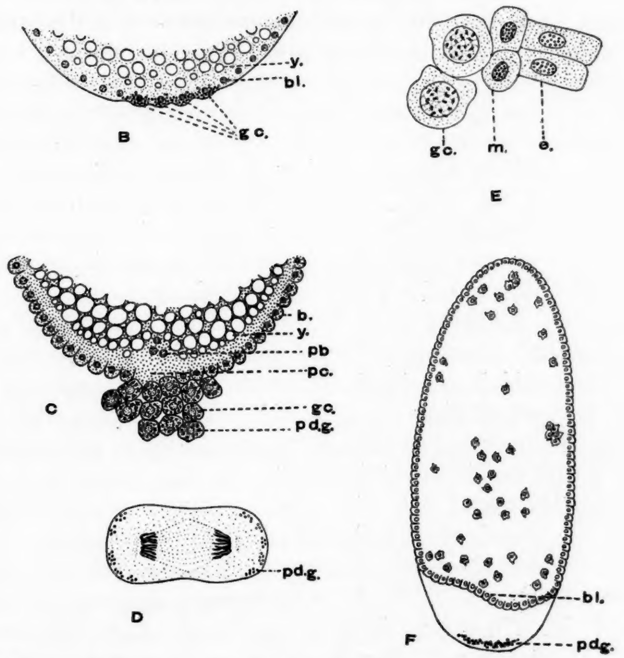

FIG. 6. Origin of the primordial germ cells in chrysomelid beetles. *A*, longitudinal section through a freshly laid egg of *Call.grapha bigsbyana*, showing pole disc (*gc.d*) at posterior end. *B*, longitudinal section through the posterior end of an egg of *C. multipunctata* eighteen hours after deposition, showing pole disc granules within the primordial germ cells (*gc*). *C*, longitudinal section through the posterior end of an egg of *C. bigsbyana* twenty-four hours after deposition, showing the primordial germ cells containing pole disc granules (*pd.g*). *D*, a primordial germ cell of *C. multipunctata* in anaphase of mitosis; the pole disc granules (*pd.g*) are apparently equally distributed at either end. *E*, two germ cells (*gc*) and neighboring mesoderm cells (*m*) and ectoderm cells (*e*) from an embryo of *C. multipunctata*. *F*, longitudinal section through an egg of *Leptinotarsa decemlineata* twenty-four hours after the posterior end had been killed with a hot needle, thus preventing the pole disc granules (*pd.g*) from taking part in the development. No germ cells are formed (compare with *C*). *bl* = blastoderm; *e* = ectoderm cell; *gc* = germ cell; *gc.d* = germ cell determinants; *gn* = conjugating pronuclei; *khbl* = keimhautblastem; *m* = mesoderm cell; *p* = posterior end of egg; *pbl* = pseudoblastodermic nuclei; *p.c* = pole cell canal; *pd.g* = pole disc granules; *vm* = vitelline membrane; *y* = yolk.

uated near the posterior end of the ventral groove. Then they separate into two apparently equal groups, one on either side of the embryo, which are soon recognizable as the two germ glands.

Because only those cells which gather in the pole disc granules become germ cells, I have called these granules "germ cell determinants" (Hegner, '08). This term has been objected to by Wieman ('10) because "the term implies the attribute of certain potentialities that these granules have not been shown to possess" (p. 180). The morphological evidence is, I believe, strong enough to warrant the use of the term; recent experiments, however, add to the convincing facts already published (Hegner, '08, '09). It is possible to show that if the pole disc is prevented from taking part in the development of the egg, no germ cells will be produced. Attempts to extract the pole disc by means of pricking the freshly laid egg and allowing them to flow out were only partially successful (Hegner, '08). A new method was later employed which absolutely prevented the cleavage nuclei from encountering the pole disc. In these experiments the posterior end of the egg was touched with a hot needle and that portion containing the pole disc was killed. In every instance the development continued and in the eggs so far examined the blastoderm formed normally over all of the surface except at the posterior end; here it was built at the end of the living substance as shown in Fig. 5, *F, bl.* No germ cells were produced. I conclude from this that the pole disc granules *are* necessary for the formation of germ cells, and that they are really "germ cell determinants." Of course it might be argued that some other substance lying at the posterior end of the egg is responsible for the differentiation of the germ cells, but this seems highly improbable. Wieman ('10) states that in *Leptinotarsa signaticollis*, a species I have not studied, "the granules are not all taken up by the cells in their migration and the greater part of them remains behind after the cells have passed through" (p. 186). This is certainly not the case in the many eggs that I have examined, and a reexamination

shows that only a few of the pole disc granules remain in the egg after the germ cells are formed, as was clearly pointed out in a former paper (Hegner, '09, Plate II, Fig. 16).

The origin of the pole disc granules is not known. It seemed to me probable that they came from the nucleus of the egg just before maturation and consisted of nuclear material. This conclusion was reached (1) because these granules stain like chromatin, (2) because in many insects the nucleus of the oogonium casts out chromatic material (Nebenkerne), and (3) because the substance which determines the germ cells in *Ascaris, Cyclops* and *Oophthora* is of nuclear origin, and in one case (*Ascaris*) is chromatin. Wieman believes that "the granules of the pole disc consist of particles derived from the food stream of the ovum that form an accumulation in the protoplasm in its posterior part" (p. 187). This possibility was pointed out in a former paper (Hegner, '09, p. 274), a fact Wieman seems to have overlooked. It was also suggested in the same place that if the granules are derived from the nurse cells they probably come from the nuclei of these cells. The pole disc granules gradually disappear after the germ cells are formed.

It may be of interest to mention the results of operations performed upon eggs in which the germ cells had already differentiated at the posterior end (Fig. 5, *C*). Such eggs, when touched with a hot needle, continued to develop, and produced embryos and larvæ without germ glands. This I believe is the earliest stage on record on which surgical castration has been performed.

The visible presence of germ cell determinants in the primordial germ cells of the animals described above suggests two possibilities as to their importance: (1) They may represent idiochromatin, *i. e.*, germ plasm, or (2) they may influence the metabolism of the cells and thus determine their character.

1. The history of the germ cells in chrysomelid beetles illustrates in a remarkable way the theory of germinal continuity as expressed by Weismann ('04). Weismann believes with Nägeli that "there are two great categories

of living substance—hereditary substance or idioplasm, and 'nutritive substance' or trophoplasm, and that the former is much smaller in amount than the latter" (Weismann, '04, Vol. I, p. 341). The idioplasm of the germ cells he calls germ plasm, a substance which is "never formed *de novo,* but it grows and increases ceaselessly; it is handed on from one generation to another like a long root creeping through the earth, from which at regular distances shoots grow up and become plants, the individuals of the successive generations" (Vol. I, p. 416). "This splitting up of the substance of the ovum into a somatic half, which directs the development of the individual, and a propagative half which reaches the germ cells and there remains inactive, and later gives rise to the succeeding generation, constitutes *the theory of the continuity of the germ plasm* (Vol. I, p. 411). According to this theory, the body or somatic cells serve only to protect, nourish and transport the germ cells which contain the germ plasm. Later the germ cells separate from the body and develop into new individuals and the body subsequently dies.

In the eggs of chrysomelid beetles the germ cells are formed at an extremely early period in embryonic development. They separate entirely from the embryo and come to lie in a group at the posterior end; at this time germ cells are quite distinct from somatic cells. Later the germ cells migrate back into the embryo, where they are protected, nourished and transported until they become mature, leave the body and give rise to a new generation.

What particular part of the germ cell represents the idioplasm or germ plasm? is a question of fundamental importance. Weismann recognizes the chromosomes as the germ plasm and has built up a complex theory as to the constituents of these bodies. The present discussion is not concerned in any way with the structure of the germ plasm as conceived by Weismann, and the writer does not wish to become involved in a consideration of idants, ids, determinants and biophores. The theory of dichromaticity (Dobell, '09) may aid in answering this

question. This theory holds that the chromatin of the germ cells is of two kinds—(1) idiochromatin, which is for reproductive purposes, and (2) trophochromatin which performs vegetative functions. In many Protozoa these two kinds of chromatin are separate throughout the life cycle. For example, in *Paramecium* the micronucleus is thought to represent the idiochromatin, the macronucleus, the trophochromatin (Calkins, '09). During conjugation and the subsequent reorganization of the nuclear apparatus the macronucleus breaks down and disappears, whereas the micronucleus gives rise not only to new bodies like itself, but also to new macronuclei.

In most animals idiochromatin and trophochromatin are supposed to be contained in one nucleus and are indistinguishable except in a few cases during the differentiation of the germ cells at an early developmental period of the egg. One is tempted to interpret as idiochromatin (1) that part of the chromosomes of *Ascaris* which is lost by the somatic cells (Fig. 1, *B, c*) but retained by the germ cells, (2) the nuclear material which is present in the primordial germ cell of *Cyclops* (Fig. 2, *B, ak*) but is absent from the somatic cells, (3) the similar substance in the primordial germ cells of *Oophthora* (Fig. 4, *n*), (4) the "besondere körper" in the egg of *Sagitta* (Fig. 3, *x*), and (5) the pole disc in the eggs of chrysomelid beetles (Fig. 5, *A, gc.d*).

One difference between these substances and the germ plasm as Weismann conceives it should be pointed out. In the cases cited above the material interpreted as germ plasm is only in one instance chromatin, and in this animal (*Ascaris*) it does not constitute the entire chromatin as Weismann's theory demands. If these extra nuclear bodies really represent the iodioplasm our location of the germ plasm must be transferred from the chromosomes to this material.

2. The second theory mentioned above, namely, that the extra material possessed by the germ cells determines these as such because of some fundamental principle of metabolism, seems more plausible than the theory just outlined. It is worthy of note that the primordial germ

cells of several animals belonging to widely separated groups are supplied with extra nutritive material. This is true in the Diptera, *Chironomus* (Weismann, '63) and *Simula* (Metschnikoff, '66), in the Lepidopteron, *Endromis* (Schwangart, '05), in the Elasmobranchs (Beard, '02), in the Teleosts (Eigenman, '92), in the Amphibia (Nussbaum, '80), and in the Reptilia (Allen, '06).

It has already been pointed out (Hegner, '09) that the pole disc granules may be nutritive material. "That the pole-cells need special means of nourishment is doubtless the case, for contrary to the condition in the blastoderm cells, they are at an early period entirely separated from the yolk, and later use up energy in their migration" (p. 275). If this is true, and as Wieman ('10) claims, the pole disc granules are derived from the yolk stream, our germ cell determinant hypothesis is not weakened, but gains a distinct argument in its favor.

It is interesting to note in this connection that two of the foremost investigators of the relation of the accessory chromosomes to sex determination are inclined to believe in the quantitative hypothesis, *i. e.*, that the egg which is fertilized by the spermatozoon containing the accessory develops into a female because there is more chromatin present, and that this plus amount influences the metabolism of the cell and its descendants (Wilson, '10; Morgan, '10). This hypothesis suggests the theory of sex advocated by Geddes and Thomson ('89), that "the female is the outcome and expression of preponderant anabolism, and in contrast the male of preponderant katabolism" (p. 132). In *Sagitta* (Elpatiewsky, '09), however, it is the male primordial germ cell and not the female that acquires the larger part of the "besondere körper."

Although neither of the two possibilities advanced in the foregoing pages may be correct, nevertheless it seems certain that the peculiar bodies in the primordial germ cells of the animals described above should be named "germ cell determinants." In any event, the attention of investigators ought to be directed toward the problem of discovering the origin and complete history of these

bodies, since their bearing upon theories of heredity is of fundamental importance.

LITERATURE

Allen, B. M., 1906. The Origin of the Sex-Cells of *Chrysemys*. *Anat. Anz.*, Bd. 29.

Beard, J., 1902. The Germ Cells. Part I. *Raja Batis*. *Zool. Jahrb., Abth. f. Anat.*, Bd. 16.

Boveri, T., 1892. Die Entstehung des Gegensatzes zwischen den Geschlechts zellen und den somatischen Zellen bei *Ascaris megalocephale*. *Sitz. Ges. f. Morph. Physiol. München*, Bd. 8.

Buchner, P., 1910. Keimbahn und Ovogenese von *Sagitta*. *Anat. Anz.*, Bd. 35.

Calkins, G. N., 1909. Protozoology. Philadelphia.

Dobell, C. C., 1909. Chromidia and the Binuclearity Hypothesis: a Review and a Criticism. *Quart. Journ. Micr. Sc.*, Vol. 53.

Eigenman, C., 1892. On the Precocious Segregation of the Sex-Cells of *Micrometus aggregatus*. *Journ. Morph.*, Vol. 5.

Elpatiewsky, W., 1909. Die Urgeschlechtszellenbildung bei *Sagitta*. *Anat. Anz.*, Bd. 35.

Geddes, P., and Thomson, J. A., 1889. The Evolution of Sex. London.

Haecker, V., 1897. Die Keimbahn von Cyclops. *Arch. Mikr. Anat.*, Bd. 49.

Hegner, R. W., 1908. The Effects of Removing the Germ Cell Determinants from the Eggs of Some Chrysomelid Beetles. *Biol. Bull.*, Vol. 16.

Hegner, R. W., 1909. The Origin and Early History of the Germ Cells in some Chrysomelid Beetles. *Journ. Morph.*, Vol. 20.

Metschnikoff, E., 1866. Embryologische Studien an Insekten. *Zeit. f. wiss. Zool.*, Bd. 16.

Morgan, T. H., 1910. Chromosomes and Heredity. *American Naturalist*, Vol. 44.

Nussbaum, J., 1880. Zur Differenzirung des Geschlechts im Thierreich. *Arch. Mikr. Anat.*, Bd. 18.

Schwangart, F., 1905. Zur Entwicklungsgeschichte der Lepidopteren. *Biol. Centralbl.*, Bd. 25.

Silvestri, F., 1908. Contribuzioni alla conoscenza biologica degli Imenotteri Parassiti. *Boll. Lab. zool. gen. e agraria. Portici*, Vol. 3.

Stevens, N. M., 1910. Further Studies on Reproduction in *Sagitta*. *Journ. Morph.*, Vol. 21.

Weismann, A., 1863. Die Entwicklung der Dipteren im Ei. *Zeit. f. wiss. Zool.*, Bd. 13.

Weismann, A., 1904. The Evolution Theory. 2 vols. London.

Wieman, H. L., 1910. The Pole Disc of Chrysomelid Eggs. *Biol. Bull.*, Vol. 18.

Wilson, E. B., 1910. The Chromosomes in Relation to the Determination of Sex. *Science Progress*, Vol. 5.

FURTHER OBSERVATIONS ON THE POSE OF THE SAUROPODOUS DINOSAURS

OLIVER P. HAY

WASHINGTON, D. C.

SINCE the publication[1] of my paper on the manner of locomotion of the Sauropoda a number of communications have appeared which treat of the same subject. Two of these I wish especially to notice here, both of which have appeared in the AMERICAN NATURALIST, one of these being written by Dr. W. J. Holland;[2] the other by Dr. W. D. Matthew.[3] A third interesting and instructive paper, from the pen of Dr. O. Abel, appeared in March, 1910, in the *Abhandlungen der k. k. zool.-botan. Gesellsch. in Wien,* Volume V, Heft 3, pp. 1–60.

Dr. Holland experiences many difficulties in his attempts to articulate the bones of *Diplodocus* so as to give the animal a pose like that of the crocodile and of the lizard. His Fig. 9, on page 268 of his communication, is intended to illustrate some of his perplexities. "Of what earthly use," he says, "the hind limb of the *Diplodocus* could have been to him in such a position I leave you to determine for yourselves." Now, although the proximal ends of those femora are not all placed as they are in the lizard or the crocodile, nevertheless, taking them as Dr. Holland has placed them, it is difficult to see why, if they were not ankylosed with the pelvis and the animal had not contracted locomotor ataxia, it could not lift itself out of the hole provided for it. Furthermore, it is not necessary for lizards to carry their knees above the level of their backs; no more was it necessary for sauropods to do this. Dr. Holland finds trouble also at

[1] *Proc. Washington Acad. Sci.,* XII, 1910, pp. 1–25.

[2] AMER. NATURALIST, XLIV, pp. 259–283.

[3] AMER. NATURALIST, XLIV, pp. 547–560.

the knee-joint, when the leg is flexed, as shown in his Fig. 11, in which case, as he states, the tibia and the fibula come into contact with the condyles of the femur at two points not larger than as many sixpences. But we must suppose that the *Diplodocus* did sometimes lie down, and in so doing did bend its legs as much as Dr. Holland has represented, or more. Whoever has observed the effort required by a horse in regaining a standing posture can imagine the strain that would come on those femoral condyles and lower leg bones when the reptile endeavored to get on his feet again; but we can hardly suppose that the bones and cartilages of the knees were crushed every time the animal arose from its slumbers. Dr. Holland appears not to appreciate the fact that all these articular surfaces were invested with abundant cartilage.

Dr. Holland's Figs. 15 and 16 illustrate the embarrassments encountered by him in his efforts to adapt the bones of the fore leg to the positions that they have in the lizard. He would have had fewer difficulties had he not been laboring under the misapprehension that the upper end of the radius articulated with the inner condyle of the humerus instead of the outer. Such a transposition of the radius and ulna would present something unique in anatomy and, in the case of the sauropods, would be wholly unnecessary.

From the compressed form of the body of *Diplodocus* Dr. Holland has derived an argument against the proposition that the reptile had a creeping mode of locomotion. Dr. Abel also formulates the generalization that among the reptiles which in locomotion do not lift the belly and thorax from the ground but drag it, the cross-section of the thorax is transversely oval. It is true that most creeping animals have the body depressed, but they vary greatly with respect to the amount of depression. On the other hand, there are lizards which have the body strongly compressed and which nevertheless progress as do other lizards. A species of the genus *Gonyocepha-*

lus shown me by Dr. L. Stejneger has the thickness of the body only .57 of the height; so that it is nearly as much compressed as Dr. Holland has represented *Diplodocus* to be. Various other genera of lizards include species with much compressed bodies. Some of the tortoises belonging to the genus *Testudo* have the shell about twice as wide as high, while in *T. abingdonii*, from the Galapagos Islands the shell is fully as high as wide. Nevertheless, this tortoise shows no tendency to assume a mammalian gait. I see no reason why, if the necessities of the animal required it, the shell might not, in the course of time, become still higher.

It is of great value to have, from one so competent as Dr. W. D. Matthew, a statement regarding the value to be attached to the form of the femur in relation to the pose of the sauropods. Dr. Matthew seems to agree with me that straightness alone of the femur does not prove that these animals walked erect on either two or four legs, only, he appears to hold that the larger mammals and dinosaurs have in general straighter femora than their smaller and more agile ancestors. This statement is, of course, subject to the condition that the femur was not straight in the ancestors themselves. And when we come to apply the statement to the dinosaurs we are likely to dispute whether the femora of *Tyrannosaurus* are or are not less curved than those of some earlier dinosaurs. Dr. Matthew describes the hinder limb of the elephant and asserts that all gigantic mammals show some approach to this type; also, that in the sauropods the resemblance in form and proportion of the hinder limb to that of the elephant is very marked. However, a number of the genera that he mentions as illustrating his views seem to me not to conform well to the specifications. *Titanotherium* does not, if we may rely on the restorations,[4] have post-like legs nor, in comparison with the elephant, short feet. *Coryphodon* does not have straight legs,[5] nor is it a gigantic mammal, being ex-

[4] *Bull. Amer. Mus. Nat. Hist.*, VII, pls. VIII, X, XI.

[5] *Bull. Amer. Mus. Nat. Hist.*, X, pl. X.

ceeded in size by some of the rhinoceroses, which again have very angulated legs. It is to be noted, too, that most of the genera mentioned by Dr. Matthew as being gigantic mammals of diverse stocks are extinct, and there might be some differences of opinion as to the exact form of their legs and even of the feet.

Nor is it certain that the type of limb found in the elephant is the result of the great size of the animal. The limb has probably not changed greatly since Middle Eocene times, when elephants were small animals; although its angulation has probably become somewhat reduced, the femur relatively somewhat longer, and the digits a little shorter. The femur of *Mœritherium,* supposed to be a relative or even an ancestor of the elephants, from the Middle Eocene of Egypt, is only eleven inches long and is as straight as that of the living elephant. The type of leg possessed by the elephant is rather primitive in its structure and is found in such animals as are slow of movement. All animals have some means of protecting themselves more or less effectively from their enemies. Horses, deer and oxen have developed angulated limbs, with short humeri and femora and elongated metapodials, combinations that confer the power of rapid flight. The elephants have found their safety in their great size; and extensive modifications of their legs have not been required.

As is well known, the lizards have straight-shafted femora, which are longer than the tibiæ, and the digits are long. As, however, the land tortoises may have short digitigrade feet, it is difficult to see why some lizards might not develop such feet. And it is not improbable that such a lizard might attain a great size and continue to retain its straight femora, short feet, and angulated limbs.

In short, it seems to the writer that Dr. Matthew's proposition as regards the significance of the straight femur is loaded with so many conditions and subject to so many exceptions, known and supposable, that it must

be applied with great circumspection to the dinosaurs.

It is frequently asserted that the pelvis and the limbs of the diplodocus possessed analogous resemblances to those of the elephant. In the pelvis these are confined, I believe, to the great size and to the convex iliac crest. In the sauropod the ilia are directed from front backward; in the elephant almost transversely. The pubes and ischia in the two animals are utterly different. The acetabula are different in form, size and position. The femora of the two animals are alike large and straight-shafted. That of the sauropod, however, has no great trochanterial process; and whether, as my critics contend, only the inner angle of the proximal end of the femur or, as I insist, the whole of the proximal end, is to be regarded as the head of the bone, this head is very different from that of the elephant. The size of the radius relatively to the ulna and of the fibula to the tibia is very different in the two animals. The digits of the elephant, in general, are far less reduced than those of the sauropod. That the limbs of the sauropods were straight like those of the elephant has been assumed; but we are now discussing that proposition.

On the outer border of the upper end of the femur of *Diplodocus* is a rugose area which extends downward a distance equal to one fifth the length of the bone, perhaps somewhat more. This, or at least its lower end, represents the trochanter major. According to Dr. v. Huene's figures, this trochanter occupied about the same level in the Triassic dinosaurs, but it was placed somewhat more on the dorsal surface of the bone. Osborn[6] represents this trochanter in approximately its correct position, but not extended far enough downward, as is evident from the photograph reproduced on his Plate XXIV. Dr. Matthew speaks of this trochanter as a "clearly marked rugosity around the proximal external angle of the head." I find this rugose surface on other sauropod femora. The upper half of a large femur in

[6] *Mem. Amer. Mus. Nat. Hist.*, I, p. 210, Fig. 14.

the U. S. National Museum measures 510 mm. across the bone just below the rough proximal end. On the fibular border the rugose surface that represents the great trochanter runs down on the bone a distance of 390 mm. At this point there is a decided angle in the border on the bone. A rough surface just like this in position and extent is found on the femur of the crocodile.

This being settled, we may turn our attention to what Marsh and Hatcher called the great trochanter, the outer half, or nearly as much, of the rough proximal end of the femur. Those who do not believe that this formed a part of the head of the bone and was not inserted in the acetabulum ought to explain what it represents.

As regards the distal end of the femur of *Diplodocus,* I do not see in what way it is essentially different from that of the lizard. Dr. Matthew says that in the latter the distal articulation for the tibia and the fibula are on the back of the femur, not on its end. As I see the femur of *Diplodocus* and that of the lizard, both have a broad articular surface on the end; and this surface is continued around on the ventral side of the bone, being there divided into two parts by the intercondylar fossa. It must not be supposed that I see no differences among the femora of the diplodocus, the crocodile and the lizard; but these are much nearer one another than that the diplodocus is to the femur of the elephant.

Dr. Holland has made the objection that in articulating the leg bones of *Diplodocus* so that there might be a right angle between the femur and the tibia there would be no surface against which the end of the femur might articulate. However, the same condition would exist in the flexed knee of the horse or of man were it not for the patella. In the flexed knee of the lizard and of the crocodile the end of the bone is covered by the tendon of the extensor muscle and the ligaments; and certainly the same was true in the sauropods. On account of the deep body of *Diplodocus* it would not probably often happen that the angle between the femur and the tibia

would be less than a right angle. When the leg was extended forward it would be nearly straight and again straight when directed backward. Also, the body would be lifted somewhat. It is an erroneous idea, held apparently by both Dr. Matthew and Dr. v. Huene, that in walking the crocodiles, lizards and turtles do not lift the body from the ground. Probably all do so; even the gigantic Galapagos tortoises carry their bodies free from the ground.

Inasmuch as the arrangement of the bones of the fore leg has been brought into this discussion, I shall make a few remarks on the subject. Few of the figures of the humerus give a correct notion of its form. Those published by Osborn and Granger[7] show well the characters of the bone, seen from the front only, in three genera of sauropods. A humerus in the U. S. National Museum, supposed to be that of *Diplodocus*, has the proximal border broad and convex and very rough, showing that it was covered by cartilage and doubtless formed a continuous articular surface. This surface played in the glenoid fossa or notch of the shoulder girdle. About the middle of this convex surface the bone is much thicker than at the ends and the thickening is on the dorsal face of the bone. This thickened portion quite certainly corresponds to a rounded elevation seen on the upper surface of the proximal end of the humerus of the crocodile, and this in its turn is probably homologous with the more narrowly limited head of the humerus in mammals. In the crocodile this elevation fits well into a depression in the scapula, in the roof of the glenoid fossa. When, however, the leg is brought well forward the elevation slips out of the glenoid notch and a part of the head farther forward takes its place and supports the weight. I believe that the same movements took place in *Diplodocus*.

Now, in the restoration of *Diplodocus* in Pittsburgh and in that of *Brontosaurus* in New York, the humerus is placed in the glenoid notch in an approximately verti-

[7] *Bull. Amer. Mus. Nat. Hist.*, XIV, p. 203.

cal position, with the deltoid border directed outward. the opposite border inward, and the primitively dorsal surface directed forward. This leaves the inner, prob ably lesser, tuberosity projecting far within the inner surface of the shoulder girdle. An examination of a lot of mounted skeletons will show that in all mammals that walk by moving the limbs in sagittal planes the inner tuberosity is greatly reduced and removed to a position in front of the head of the bone, and little or none of the humerus projects beyond the inner surface of the scapula. In two mammals I find a large process which corresponds, in position at least, to the inner one of the sauropods. These are the echidna and the duck-bill, and both of these mammals move the legs as the creeping reptiles do. I believe that the prevailing manner of articulating the humerus of the sauropods is wrong. It ought to be placed in a plane approximately horizontal, with the lower and upper faces in their primitive positions, with the deltoid border forward, and, when the leg is in a median position of its swing, with the thickening of the proximal articulatory surface in contact with that part of the glenoid notch that is formed by the great ridge that passes across the scapula. In case the leg is placed further forward or further backward, corresponding parts of the convex articular end of the humerus ought to pass under this ridge. There was no need at any time of life that the lesser tuberosity should project against the ribs or into the muscles. The arrangement that I have described is that which may be observed in the crocodile also.

If now the ulna and the radius are articulated properly with the humerus the whole leg will function as it does in the lizard and the crocodile. In the U. S. National Museum is a specimen, shown me by Mr. Chas. W. Gilmore, which consists of the radius and the ulna, somewhat crushed, but preserving nearly their original relations to each other. These bones differ somewhat from those of the crocodile, as might be expected. The

principal difference is found in the fact that the upper end of the ulna extended across the lower end of the humerus and has a concavity in front for the head of the radius. The ulna and radius appear to have been more closely bound together at the lower ends than in the crocodile; nevertheless, the bones of the two reptiles resemble one another closely. When to those of the sauropod a humerus of corresponding size is fitted, with the outer (anterior) condyle in contact with the head of the radius, the leg is strikingly like that of the crocodile. In my opinion, Marsh's arrangement of the bones of the fore leg of *Brontosaurus*[8] is more nearly correct than later restorations of this limb in the same animal and in *Diplodocus*. In the figures referred to, the humerus, in the middle of the step, presents the dorsal surface outward; whereas, in the Pittsburgh and New York restorations this surface looks backwards and the deltoid border looks outward. If Marsh's figure were modified so that the humerus were horizontal or nearly so, the leg would have nearly its natural position.

Various opinions are held regarding the question whether the sauropods were strictly aquatic, strictly terrestrial or amphibious. In my paper published in the *Proceedings of the Washington Academy of Science* I called attention to a figure that illustrates Cope's views and to another published by Matthew that elucidated Osborn's ideas. Dr. Matthew's views seem to differ from those of Osborn in that the former maintains that these reptiles usually preferred not to be wholly submerged and that they could not leave the water without endangering the integrity of their limbs. He finds his reasons for his opinion as to the depth of the water preferred in the fact that the bones above a line drawn from the hip joint to the shoulder blade are of light construction, while those below this line are thick and heavy. This line is his "water-line" and indicates the average depth of the water haunted by these reptiles. The heavy

[8] The Dinosaurs of North America, Pl. XLII.

bones of the legs were intended, according to Dr. Matthew, to hold the animal down in the water, as the lead in the diver's shoes holds him on the bottom. However, it occurs to the present writer that if the sauropods were accustomed to wade in water that came only a little more than halfway to their backs the weight of the unsubmerged part of the body would suffice to hold them to the bottom. A man who wades in water only waist-deep does not need leaden soles. To maintain the theory, it seems necessary to keep the reptiles more deeply submerged. To do this it is only necessary to suppose that they crawled about at the bottom of the water as crocodiles do. If we suppose that the sauropods walked wholly submerged and erect on four legs the differentiation observed by Dr. Matthew in the ossification might be explained on the supposition that it was for the purpose of ballasting the animals. However, it does not appear that the hippopotamus, an eminent wader, needs to be steadied in this way. Furthermore, why should it have disturbed such facile swimmers as the sauropods probably were to heel over occasionally?

Notwithstanding the means employed by nature to reduce as much as possible the weight of the skeleton, the bodies of the sauropods were very heavy. The bones of the legs were well-developed and I recognize that they were not as hollow as those of a horse, for example. Can we not, after all, most reasonably explain the case by supposing that the sauropods went about more or less on land and needed strong legs to hold up their heavy bodies?

In my former article I expressed the opinion that it was hardly possible for a diplodocus to walk about wholly submerged. It appears that Cope and Osborn and Matthew have thought that the animal would have no difficulty in doing this. Perhaps the question can never be definitely decided. The hippopotamus is said to walk beneath the water and probably does really do so; at least they remain for considerable periods be-

neath the water and move about. They are active swimmers and it is possible that their movements along the bed of the river or lake are to a considerable extent due to the action of their feet against the water. They have massive skeletons which have evidently been developed to bear them down in the water. Nevertheless, it is to be questioned whether the animal exerts any considerable pressure on the bottom. If the specific gravity were any considerable amount above that of the water the animal would have difficulty in coming to the surface for air and to get a view of its surroundings. Tapirs too are said to be great swimmers and divers and to run along on the bottoms of streams; but these mammals have no special modifications of the skeleton to enable them to do this. Possibly they lay hold of the bottom in some way with their hoofs, or, while running they may incline the head and body downwards and forwards, like a descending aeroplane. That the hippopotamus with his heavy skeleton has a specific gravity little above the water is proved by the following fact related in Brehm's Thierleben: When a hippopotamus is killed he at once goes to the bottom. Nevertheless, in many cases the body comes to the surface within from 30 to 60 minutes, a result of the development of gases within the cadaver. Hence, it is extremely doubtful whether the animal can exert much pressure on the bed of the stream. So too, even if the sauropods did walk about at the bottoms of streams, wholly submerged, they must have rested there very lightly.

Now what conclusions can we draw from the facts above established? Dr. Matthew's strongest argument in favor of the erect pose of the sauropods is derived from the supposed resemblance of their limbs to those of the elephant, the long straight femur, the short digitigrade feet, and the slight angulation of the limb. "Obviously," says he, in describing rectigradism, "a specialization of this kind will occur only in an animal which habitually rests its weight on the limbs." But we are

dealing here with animals that are supposed to have the whole, or at least nearly the whole, of the weight taken from their limbs.

Moreover, does not the one part of Dr. Matthew's theory contradict the other? He has told us that the parts of the skeleton below the water-line were heavy for the purpose of overcoming the buoyant effect of the water, as the lead in the diver's shoes does. Then, as shown in the preceding paragraph, he maintains that there was pressure enough to produce such legs as the elephant has, an animal whose legs must support its whole weight.

We may now be permitted to inquire whether or not aquatic life is likely to have produced either of the effects attributed to it by Dr. Matthew. The hippopotamus is an animal far less aquatic than Cope and Osborn and Matthew have supposed the sauropods to have been. Its limbs are almost ridiculously short, so short that when it is quitting or entering the water its belly leaves broad and deep channels in the mud through which it wades. The leg bones are indeed very strong, a result conditioned by the frequent excursions made on the land. The feet are the most primitive possessed by any living artiodactyl, and the digits are bound together by a short web. The aquatic performances of the tapir have not contributed to its structural uplift, for its feet are among the most primitive of those of the perissodactyls. Let one only view with some attention a series of mounted skeletons and one will soon be struck with the fact that degenerative changes begin to affect the limbs of animals very shortly after they begin to confide to the water the support of their bodies; and these degenerative modifications continue to manifest themselves until the limbs have been converted into paddles and flippers or reduced to vestiges or even extirpated.

That the sauropods had originally been amphibious and then became strictly aquatic seems to the writer highly improbable. Those short digitigrade feet, with

toes having a reduced number of phalanges, seem to furnish almost positive proof that their possessors had for many generations been accustomed to travel on solid ground. It is probable that their resort to the water had not endured long enough yet to affect to any great degree their organization, except as to size.

Dr. Matthew believes that at some stage the ancestors of the sauropods were bipedal and that later they became secondarily quadrupedal. He grants that the indications of former bipedalism in this group are less apparent than in the quadrupedal Predentata. It is easy to agree with the latter opinion. As to the hinder limbs, we ought to expect that bipedal locomotion would have led to the development of smooth, well-finished articular surfaces and of a trochanter major standing out as a distinct process near the upper end of the femur. Why, on the resumption of quadrupedal locomotion, should these acquisitions have disappeared as if they had never existed? This has not happened even in the walruses, seals, porpoises and manatees, which forsaking the land, have betaken themselves to the water. The inevitable result, if not the prerequisite, of bipedalism is a considerable reduction in the size of the fore legs and various transformations of the hands. But the fore limbs of *Diplodocus* and of *Brontosaurus* show no reduction in size. Are we to suppose too that while the fore legs were held from contact with the ground and were probably employed for other purposes than locomotion, they continued to progress in digitigrady? Those fore feet look as if they had been walked on fully as much as the hinder feet.

From a photograph of the fore foot of a *Diplodocus* in the American Museum of Natural History Dr. v. Huene concludes that this foot was exaxonic. It would be interesting to learn more about this foot, especially whether or not the bones were found in their natural relations. The foot differs from that of some other sauropods, certainly. With the ulna and radius before

mentioned, in the U. S. National Museum, there are present all the metacarpals and some of the phalanges. Through pressure two of the metacarpals, the fourth and the fifth, have had their hinder faces squeezed against the hinder faces of the other three. Otherwise, the bones retain their original relationships. Of these the first is distinctly larger than the fifth. The lower end is especially enlarged, to support the phalanx and the great claw. It is proper here to say that Dr. v. Huene has very justly criticized the representation of the feet of *Diplodocus* as presented in my plate published in the *Proceedings of the Washington Academy of Science.*

Dr. Matthew refuses to accept my explanation of the tracks made by the supposed iguanodon. Those tracks are certainly in need of explanation. So far as I am aware, no one has as yet ventured to mount a dinosaur with the toes pointing inward after the manner of those tracks.

Neither does our author accept my suggestion that some of the tracks found in the Triassic sandstones of the Connecticut River Valley were made by birds. The conclusion appears to be that, because a few dinosaur *bones* have been found in that region, therefore all the *tracks* are those of dinosaurs. Dr. Matthew does not attempt to show how animals built as were the Triassic dinosaurs that we know, with short diverging femora, rather short lower leg bones, and short metatarsals, could put one foot directly before the other in walking or running. It is much to be doubted whether a running duck or penguin could do this. And are we to suppose too that those Triassic dinosaurs were always running? It may be easy in mounting the skeleton of a dinosaur to place the femora parallel or even to bring the knees together. In life the thighs could not take this position, unless on each side there had been a considerable excavation at the junction of the ponderous belly and the thick tail, a sort of little wheel-house for the thigh to

play in. It seems quite doubtful whether the carnivorous dinosaurs of even the Jurassic period had the erect bird-like bearing that is usually attributed to them. The extraordinary development of the pubic bones of *Ceratosaurus,* whose expanded and ankylosed distal ends reached nearly half-way to the fore legs, seems to me to indicate that these animals, when in repose, had a prone position, resting much of the weight on the pubes, and that when running their legs straddled considerably.

Dr. Matthew thinks that the sauropods had too great a bulk to have lived on land. The law to which he gives expression does, of course, prescribe a limit to the size an animal can attain, but who has yet determined what that limit is? Larger elephants have lived than those now living, and it is not certain that we have discovered yet the largest that have lived. Animals do not attain a great size simply to test the laws of mechanics.

SHORTER ARTICLES AND CORRESPONDENCE

COMPUTATION OF THE COEFFICIENT OF CORRELATION

In Dr. Harris's recent note[1] suggesting a helpful modification of the method of computing the coefficient of correlation, the only objection mentioned is the fact that his method results in very large product-numbers. This difficulty can be considerably reduced by a procedure based on the fact that the calculation of the standard deviation and the coefficient of correlation does not depend upon the absolute dimensions of the things measured. All that is required is a given series of successive grades; the standard deviation will then be obtained in terms of the units separating the grades, whatever they are; while the coefficient of correlation is a relative number, quite independent of the value of the units. We may therefore give to the lowest grade of both sets of measurements (x and y) the value 0, for the succeeding ones the values 1, 2, 3, 4, etc., instead of the real values; the labor of computation will then be greatly reduced, while the same value will be found for the two constants in question. The values which Dr. Harris calls A_x and A_y will by this method not be the means of x and y (so that they may well be designated rather d_x and d_y), but the means can be obtained from them without labor by simply adding to each the absolute value of the lowest grade of x and of y, respectively (since we had reduced all grades by this amount, in substituting 0 for the lowest grade).

This much simplifies the computations when the absolute dimensions are represented by numbers considerably greater than unity. Thus, in Dr. Harris's Table III., in finding the standard deviation we should for the third grade have to multiply by but 4, instead of by the square of 28.

H. S. Jennings

NOTE ON BATRACHOSEPS ATTENUATUS ESCH.

Batrachoseps attenuatus is the most abundant salamander in the vicinity of Stanford University. During the rainy season

[1] This journal, November, 1910.

it can be found under nearly every rock and log on the neighboring foothills. No one has, so far as I am aware, discovered and described its egg-laying habits. The author obtained some of the eggs of this salamander and the following brief note is published with the hope that it may attract the attention of some student to this problem.

The first eggs obtained were discovered by T. Kimura during January, 1906. They were found partly buried in depressions under rocks on a moist hill side. On January 5, 1907, the author found some eggs under a log in a moist ravine well up in the hills. The eggs were deposited in small pockets in the ground; 21 were in one group and 10 in another group about 2 feet distant, while 4 were scattered between, suggesting that all were deposited by a single female. These eggs were round or slightly oval and about 6 mm. in diameter. Development was well advanced. The first individual to issue from the egg appeared on January 28, and was 17 mm. in length and of a dull black color. By May 22 it had doubled in length and was 35 mm. long. The majority of the eggs, when found, were covered with a fungus and failed to develop. This suggests that they may have been under abnormal conditions. It seems very likely that the majority of the eggs of this species are deposited just beneath the surface of the ground, as is the case with earthworm eggs and so escape detection. Diligent search at the proper season should settle this question.

Batrachoseps attenuatus disappears from this region with the approach of the dry season and appears suddenly in the fall after the first heavy rains. I have been informed that it can be obtained at any season in the moist coast region near Pacific Grove. It seems probable that in the dry regions this salamander burrows into the ground as the earthworm does to escape the drought. This theory is supported by the shape of the body, which is elongate, slender and roundish, suggesting that of the earthworm. It appears that we have here a parallel development of form and habit between *B. attenuatus* and the earthworm due to a struggle against the same physical environment.

C. V. BURKE.

NOTES AND LITERATURE

SOME RECENT STUDIES ON VARIATION AND CORRELATION IN AGRICULTURAL PLANTS

FROM the nature of his material the student of agricultural problems has an unexcelled opportunity to collect large masses of statistical data. Domestic animals and plants, particularly the latter, can be easily propagated in vast numbers under conditions controlled in all sorts of ways. Not only the opportunity, but also the desirability, of collecting data on a statistical scale, has been recognized by agricultural investigators from the beginning of experiment-station work in Germany, and still earlier by individual students in this field. Much of the early statistical material relating to agricultural objects or problems still remains unanalyzed and undigested, because of a lack of adequate statistical methods, on the one hand, and a lack of acquaintance on the part of the collector of the data with what mathematical methods did exist for the analysis of such material, on the other hand.

It was obviously to be expected that a system of adequate biometric methods, such as that which has been developed by Professor Karl Pearson, would in due time come to play a conspicuous part in agricultural investigations. This time is coming. One who follows the current literature of agricultural science, in a broad sense of the term, can not fail to be struck with the rapidly increasing use of these mathematico-statistical methods during the last few years. In so far as the methods are correctly and appropriately used this is a most commendable movement. But it must always be kept in mind not to let admiration for the method *per se* blind one as to the real significance and importance of the biological problem attacked. The futility of dealing biometrically with data or problems which lack a sound biological basis is obvious. The indiscriminate application of biometric methods to all kinds of data is easily seen upon critical examination, to have only so much value or validity as resides in the original data themselves. It is particularly important that this point be kept in mind in agricultural work along biometric lines, because of the great ease with which mere statistics can be collected in this field, and the consequent temptation to collect them without critical consideration of their meaning and worth.

It is the purpose of the present review to discuss some of the recent work which has been done along biometric lines with agricultural materials and on problems relating to the science of agriculture. The list of literature at the end or the review based on it does not aim at completeness either in respect to the period or the field covered. Rather it is the aim to indicate the general trend of work in this field and to discuss its points of strength and of weakness.

At the outstart should be mentioned a number of papers which have dealt with the general subject of statistical methods as applied to agricultural material. The general purpose of such papers has been, on the one hand, to call the attention of agricultural workers to the existence of such methods and to the desirability of their use, and, on the other hand, to give some account of the nature of the methods themselves. Here are to be noted the papers of Albrecht, Roemer (introductory portion), Schoute, Quante, Rietz and Smith, and Zaleskiego. The last three papers are especially worthy of attention. The paper of Rietz and Smith gives an excellent elementary discussion of correlation. It further furnishes a most hopeful sign of the rapid development in research standards in agricultural work in this country. Zaleskiego makes keen analytical use of frequency polygons in his breeding work. He calls special attention to the prime importance of not lumping together non-homogeneous material. Rather he urges studying the frequency polygon derived from the progeny of each "pure line" by itself. Then later these separate polygons may, if there is reason for it, be summed together to make a "general population" polygon. But to start with the latter and neglect the biological units (pure lines) which go to make it up is wrong. This insistence on the strict biological or gametic homogeneity of material to be studied by statistical methods is worthy of all commendation.

Quante discusses from a general standpoint some of the problems of variation in agricultural plants. He considers that a definite morphological difference is certainly present between species, varieties or groups when their means differ by five or more times the probable error. He shows that in a number of characters of barley and wheat which he studied the variation is distinctly skew. In a selected strain of rye he found clear evidence of a "normal" or Gaussian symmetrical distribution of variation.

Turning our attention next to special investigations we may

consider different crops separately and take wheat first. Here the studies of Roberts and his students take a leading position. For some years this investigator has been engaged upon a very comprehensive biometrical study of wheat. Only fragments of this work have as yet been published. We may first consider his paper on "A Quantitative Method for the Determination of Hardness in Wheat." An apparatus was devised by which the weight in grams necessary to crush a grain of wheat could be directly determined. The problem was to find out how large a random sample of kernels must be taken in order to reach a reliable result as to mean crushing weight for a variety or strain. Samples of from 100 to 500 kernels each were tested and the mean for each sample determined, two varieties of wheat —a hard and a soft—being used. It is shown that the mean crushing weight diminishes regularly and rapidly as the size of the samples increases, until a minimum at a sample of 450 kernels is reached. Samples of 500 kernels show an increase in mean crushing weight over the 450 kernel sample. Why the *mean* crushing weight should regularly diminish with increasing size of sample is not clear, and is neither explained nor even discussed in the paper. That the *error* of the mean crushing point would diminish with increasing size of sample is obvious. The error of the mean is found, as a matter of fact, to diminish according to a hyperbolic curve. A mathematical discussion of this curve of the errors of the means is given, and examination of the second differential shows that the *rate* of diminution of the error becomes negligible after a sample or group size of 350 kernels. It is then concluded that 350 kernels is a sufficiently large sample to use practically in determining mean crushing points.

Roberts's paper on "Breeding for Type of Kernel in Wheat" is a very thorough and extensive biometrical study of the form of the wheat kernel in many different pure lines or races. Means only are given in this paper, but the amount of measuring and computing involved must have been literally stupendous. Only such a biometrical organization as that maintained at the Kansas Station could have managed it. Data are given on mean length, width, length/width index, volume, weight, and specific gravity of the individual kernel, samples of 500 kernels being taken in 5 separate 100-kernel lots for each pedigree strain (pure line). Also determinations were made of the weight of 100 c.c. of grain, of a packed and a struck bushel of grain, and of the percentage volume not occupied by grain when a 100 c.c. measure is filled

with grain. This last determination was made by the alcohol method. The upshot of this elaborate study is to show that the *shape* of the grains as measured by the length/width index is a very significant factor in determining how wheat will grade according to commercial standards. It is shown that "a difference of at least as high as three pounds per bushel may exist between different pure-bred wheats having identical average kernel-volume and kernel-weight." The final conclusion is that the percentage volume of grain in a packed measure would be a much more just and scientific basis for market grain grading than the present system of test bushel weight. This paper illustrates in a very striking way how the scientific method can solve in a precise and final manner a practical commercial problem.

Lill has made a quantitative study of the relation of size, weight and desirability of kernel to germination in wheat. His data indicate that germination capacity is not correlated with size of kernel, but is correlated with density of kernel. No biometrical analysis of the data is attempted.

Waldron has made an interesting and significant biometrical study of the correlation between weight of grain and other plant characters in oats and wheat, using his own measurements for the former cereal, and published data for the latter. He shows that in oats the mean grain weight per head is *negatively* correlated to a rather high degree with (*a*) number of grains per head, (*b*) length of head and (*c*) length of culm. This obviously leads to a somewhat paradoxical result, namely, that when plump, heavy seed is sown, it is seed which is taken from mother plants which are *below* the average in size and yield. Yet careful experiments, covering a period of years, have shown that planting heavy seed gives increased yields. In other words, a practise which amounts to continued selection of the *poorer* yielding of plants as parents results in *increased* yield in the progeny. This paradoxical result needs analysis by careful pedigree breeding.

Clark has published a general biometrical study on variation and correlation in timothy, the material being gained in connection with the extensive breeding experiments with this grass which have been in progress for some years at Cornell University. The point of chief interest and novelty in the work is that each of the 3,505 plants which furnished the data was under observation during three consecutive years. The material thus gives some basis for an estimation of the relative influence, on the one

hand, of germ-plasm (*i. e.*, germinal determinant factors of whatever sort), which presumably was identical for each plant during the three years, and environmental factors, on the other hand, in determining observed degrees and kinds of variation in the adult organism. The results taken as a whole show that what might be called the general variation *facies* of a population of *Phleum* must depend to a very high degree upon "nurture" rather than "nature." The degree of variation, the degree of skewness of the variation curves, the closeness of correlation between different characters of the plant—all these are changed by general environmental conditions to a marked extent. Thus to take an example: the coefficient of correlation between weight and height of plant is given as $.274 \pm .011$ in 1905 and as .718 in 1907. This is a *relative* change of nearly 200 per cent. In another case a significant positive correlation one year becomes significantly negative two years later. In general the heights (or weights) of timothy plants in any one year are correlated with the heights (or weights) of the same identical plants in another year only to about the degree indicated by a coefficient of around .5, which is but 50 per cent. of perfect correlation.[1] In other words, it appears on the basis of this result that in determining what a given timothy plant shall be like next year in respect to such characters as height and weight the innate constitutional, hereditary factors within the plant are on the whole of neither greater nor less importance than external environmental circumstances. In this case, and in respect to the characters dealt with, "nature" and "nurture" are about evenly balanced, with what advantage there is on the side of "nurture." The author emphasizes the practical significance of a result of this kind to the man who is carrying on selective breeding, and who obviously must make his selections at the outstart on the basis of the visible somatic characters as they are developed at the particular place and time at which he is doing his selecting. The paper is unfortunately marred by arithmetic errors.

It is a well-known fact that European workers (other than English), generally speaking, have very little acquaintance with biometric technique. A good example of this fact is afforded by a paper of Grabner on the problem of correlated variation in barley. The investigator desired to learn what relation existed between the economically valuable characters of this cereal. He collected a vast lot of statistical data regarding such characters

[1] Cf. Clark's Table VIII.

as yield of grain, hectoliter weight, weight of 1,000 kernels, size of kernel, protein content and "mealiness" or softness of grain. Instead of proceeding by the straightforward method of forming a correlation table and deducing therefrom the coefficient of correlation the author follows the laborious, inaccurate and inconclusive plan of averages. Virtually what is done is to calculate the observed regression line of one character on another. The general result reached, though in no wise critically supported by the evidence presented, is that all of the purely physical characters are correlated together to a high degree. The chemical and chemico-physical characters protein content and "mealiness" are not demonstrably (by the method used) correlated with other characters, though they are mutually definitely correlated. The chief scientific value of the paper is to illustrate in a striking manner how crude and clumsy were pre-Galtonian methods of attacking a simple statistical problem.

Turning now to corn, we have a number of studies of a more or less biometrical character. Apart from the primarily genetic studies on maize of East, Shull, Collins, and Pearl and Surface which are quantitative in character and to some extent[2] biometric in the treatment of the data, there have appeared recently two special studies on variation and correlation in this plant. The first of these is the paper of Rietz and Smith and the second that of Ewing. The objects of the two papers are apparently somewhat dissimilar. Ewing's is primarily a biological investigation, whereas Rietz and Smith apparently desire primarily to set forth the method of measuring correlation, and incidently to illustrate these principles by means of some corn data which they have on hand. The only general result of particular biological significance brought out in the work of Rietz and Smith is that the degree of correlation between various ear characters (length, circumference, number of rows, weight) is very markedly influenced by environmental conditions surrounding the growing crop. This paper is to be commended for its clear exposition of the method of calculating a correlation coefficient.

Ewing's paper contains more matter of general biological interest. Especially to be mentioned is the valuable discussion of the literature of correlation. The general problem which formed the basis of this investigation was to learn in how far the

[2] Shull gives some very interesting data in the form of variation constants (mean, standard deviation, and coefficient of variation) for variation in number of rows on ear in pure and cross-bred (F_1 and F_2) maize.

determination of statistical correlations between different parts of the maize plant might be of use to the practical breeder. The general conclusion to which the author comes in regard to this point is as follows:

> Considerable study of the subject has forced upon the writer the belief that it is improbable that much use can be made of correlation in practical breeding. There are rare cases in which the coupling of unit characters may aid the breeder in making selections at an early period, but the existence of correlation in the fluctuating variability of two different characters is not likely to prove of much assistance. Nothing more than a moderate degree of correlation is likely to be found in these cases, unless some such relation as cause and effect exists between them. This is especially true of correlation between seed production and other characters, since the former depends upon a large number of other characters and conditions.

The correlations studied were those of weight of grain per plant (measuring *yield*) with each of the following characters: (1) Diameter of stalk, (2) length of leaf, (3) breadth of leaf, (4) height of mature plant, (5) height of seedling, (6) number of internodes, (7) average length of internodes, (8) percentage of internodes below the ear, (9) length of ear at appearance of silks, (10) date of appearance of tassel, (11) date of appearance of pollen, (12) date of appearance of silks, (13) duration of flowering period (pistillate flowers) in days, (14) number of branches in the tassel.

The coefficient for correlations 1–6, inclusive, 9, 10 and 12, are, in each case, from 5 to 19 times the respective probable errors. They are thus statistically significant. In view of this fact the statement in the general discussion of results that "in most cases the coefficient of correlation is so small that it is probably not worth while to try to classify it or even to conclude that there is correlation," seems not to have been very well considered. The same criticism is to be made against the paper of Clark discussed above. These authors appear to overlook the fact that whether a correlation is statistically significant (*i. e.*, whether correlation "*exists*") depends not upon its absolute value, but upon its relation to its probable error. A coefficient of $.0009 \pm .0001$ would be to a high degree of probability *statistically* significant, though absolutely small.

The garden pea (*Pisum sativum*) has been the subject of several recent biometric studies. At the Massachusetts Station Waugh and Shaw have been for some time engaged in an

investigation of inheritance in this form, conducted along biometric lines. In their first paper here reviewed they present variation data regarding the four following characters: length of vine, number of pods per vine, length of pod, number of peas per pod, and total peas. The raw data are not given and the discussion is very meager. Graphs of the variation curves are given, but instead of making these plottings of the actual frequency data as polygons, the authors connect the plotted points by freehand sweeping curves. This is certainly a simple and expeditious, if somewhat naïve, method of curve-fitting! It is much to be regretted that such an inadequate, and indeed absolutely incorrect, method of presentation of statistical results should have been resorted to. In the discussion of heredity stress is laid upon the varying degrees of prepotency observed in the transmission of characters by individual plants. To measure this a new "coefficient of heredity" is proposed. The formula for this is

$$C = 1/\sigma D,$$

where C is the proposed coefficient, σ the standard deviation of offspring and D the difference between the parental character and offspring mean of the same character. It is obvious that the more nearly the offspring are like each other, and like the parent the larger will C become. It is somewhat unfortunate that this is called a "coefficient of heredity," since this term is in common biometrical usage for a very different constant. Indeed, in their own paper Waugh and Shaw use this term not only for their proposed constant, but also for the correlation coefficient between parent and offspring. A satisfactory measure of *individual* (not *average*) prepotency is a thing which is badly needed in breeding work. While the constant C proposed by Waugh and Shaw meets some of the conditions which such a measure must fulfill, it unfortunately appears to be of rather restricted significance and usefulness. The numerical value which it takes for different characters are not comparable one with another. The reason, obviously, is because the numerical value will change in accordance with the absolute rather than the relative variability of the character. An elephant and a mouse each equally prepotent with reference to the transmission of any character, say skull breadth, would have very different values of C for this character. Further, the constant becomes rather difficult to manage in cases of biparental inheritance, or

in those cases of undoubted prepotency, which are of the greatest interest and importance both theoretically and practically, wherein the prepotent individual does not itself have the character with regard to which it is prepotent expressed in its own soma. An example here is the dairy bull, prepotent in respect to milking qualities.

A continuation of this work on peas is reported in the second paper by the same authors. Data are presented showing the relation between observed variability and environmental (seasonal) conditions. The interesting point is brought out that there is less variation, and a higher correlation between parent and offspring, in respect to vine length, than in respect to either number of pods per vine or total peas per vine.

Roemer gives a very detailed biometrical study of pure lines in peas. The work is essentially a confirmation, with another plant, of Johannsen's epoch-making investigations on beans, though it lacks any extensive studies on the effect of selection within the pure line. The essential objective point of Roemer's research is rather to determine the biometric characteristics of pure lines as such in relation to the general population. Among the more important general results are the following:

1. The different biotypes in a population arrange themselves in frequency distributions in accord with Quetelet's law.

2. No relation was found to exist between the variability of the biotypes (*i. e.*, variation within the general population) and variation within the pure lines.

Shaw has made a very thorough biometric study of variation in the Ben Davis variety of apples and presents a mass of data of considerable general biological interest. When one recalls that commercial apple varieties are propagated by vegetative processes entirely, the importance of a careful study of this variation under different environmental conditions is obvious. Shaw shows that the mean size and shape of apples of the Ben Davis variety are distinctly different for different trees of the same orchard and even for the different parts of the same tree. There are very marked differences in apples of this variety in respect to size and shape characters when they are grown under widely different soil and climatic conditions. In the south the Ben Davis is a short round apple; in the north it is an elongated apple. Not only are the means different in different environments, but also the variability (as measured by the coefficient of variation) is changed. This paper of Shaw's, while itself purely descrip-

tive, is of great value not only for the interesting data regarding variation which it presents, but also in indicating clearly the rich reward which may be expected to follow a combined experimental and biometric attack upon the fundamental biological problem of the effect of stock on scion.

In the papers so far discussed there has been in every case some attempt at biometric analysis of the raw statistical data. There are constantly appearing in agricultural literature papers in which a great mass of first-class statistical material on variation and correlation in agricultural plants is presented but not analyzed biometrically, or only incompletely so. Examples of this are found (to mention but two) in the interesting papers of Kohler on potatoes and Westgate on alfalfa. A conspicuous instance of failure to make profitable use of elementary biometrical methods is seen in the paper of Stockberger and Thompson on hops. These authors put their data in form for calculating variation and correlation constants (*e. g.*, they give a correlation table for the correlation between number of vines to the hill and yield per hill) but do not determine the constants.

It is evident from what has preceded that biometrical methods are rapidly gaining a place among the agricultural investigator's working tools. Keeping always in mind the caution expressed at the beginning of this article that biometric zeal be not allowed to outrun biological discretion this movement merits only commendation and further encouragement. The agricultural investigator has an almost unique opportunity to make significant and profitable application of biometric methods of research.

RAYMOND PEARL.

REFERENCES TO LITERATURE

1. Albrecht, K. Die Fehlerwahrscheinlichkeitsrechnung und ihre Anwendung auf die Pflanzenzüchtung. *Fühlings Landw. Ztg.*, 1908, pp. 577–585.
2. Clark, C. F. Variation and Correlation in Timothy. Cornell Agr. Expt. Stat., Bul. 279, pp. 301–350, 1910.
3. Collins, G. N. The Value of First Generation Hybrids in Corn. U. S. Dept. Agr., Bur. Plant Ind., Bul. 191, pp. 7–45, 1910.
4. East, E. M. A Mendelian Interpretation of Variation which is Apparently Continuous. AMER. NAT., Vol. XLIV, pp. 65–82, 1910.
5. Ewing, E. C. Correlation of Characters in Corn. Cornell Univ. Agr. Expt. Stat., Bul. 287, pp. 67–100, 1910.
6. Grabner, E. Wechselbeziehungen zwischen den wertbestimmenden Eigenschaften der Braugerste. *Jour. f. Landw.*, Bd. 57, pp. 321–350, 1909.

7. Kohler, A. R. Potato Experiments and Studies at University Farm in 1909. Minn. Agri. Expt. Stat., Bul. 118, pp. 65–141, 1910.
8. Lill, T. G. The Relation of Size, Weight and Density of Kernel to Germination in Wheat. Kansas Agr. Expt. Stat., Circ. 11, pp. 1–8, 1910.
9. Pearl, R., and Surface, F. M. Experiments in Breeding Sweet Corn. Me. Agr. Expt. Stat., Ann. Rpt., 1910, pp. 249–307.
10. Quante. Variationsstatistische Untersuchungen über den Bau der Getreidearten unter Zergrundelegung der Kollektivmasslehre. Die landw; Versuchs-Stationen, 1910, pp. 121–162.
11. Rietz, H. L., and Smith, L. H. On the Measurement of Correlation with Special Reference to some Characters of Indian Corn. Ill. Agr. Expt. Stat., Bul. 148, pp. 291–316, 1910.
12. Roberts, H. F. A Quantitative Method for the Determination of Hardness in Wheat. Kansas Agr. Expt. Stat., Bul. 167, pp. 371–390, 1910.
13. Roberts, H. F. Breeding for Type of Kernel in Wheat. Kansas Agr. Expt. Stat., Bul. 170, pp. 99–138, 1910.
14. Roemer, Th. Variabilitätsstudien. *Arch. Rass.- u. Gesellsch. Biol.*, 7 Jahrg., pp. 397–469, 1910.
15. Schoute, J. C. Die Fehlerwahrschenslichkeitstheorie für die Praxis der Versuchsstationen. *Die landw. Vers.-Stat.*, Bd. LXX, pp. 161–180, 1909.
16. Schoute, J. C. Zur quantitativen Reinheitsbestimmung von Leinkuchen und Leinkuchenmehl. *Ibid.*, pp. 171–247, 1909.
17. Shaw, J. K. Variation in Apples. Twenty-second Ann. Rpt. Mass. Agr. Expt. Stat., Part I, pp. 194–213, 1910.
18. Shull, G. H. Hybridization Methods in Corn Breeding. *Amer. Breeder's Mag.*, Vol. I, pp. 98–107, 1910.
19. Stockberger, W. W., and Thompson, J. Some Conditions Influencing the Yield of Hops. U. S. Dept. Agr., Bur. Plant Ind., Circ. 56, pp. 1–12, 1910.
20. Waldron, L. R. A Suggestion Regarding Heavy and Light Seed Grain. Amer. Nat., Vol. 44, pp. 48–56, 1910.
21. Waugh, F. S., and Shaw, T. K. Variation in Peas. Twenty-first Ann. Rpt. Mass. Agr. Expt. Stat., Part II, pp. 167–173, 1909.
22. Waugh, F. A., and Shaw, J. K. Plant Breeding Studies in Peas. Twenty-second Ann. Rpt. Mass. Agr. Expt. Stat., Part I, pp. 168–175, 1910.
23. Westgate, J. M. Variegated Alfalfa. U. S. Dept. Agr., Bur. Plant Ind., Bul. 169, pp. 1–63, Pl. I–IX, 1910.
24. Zaleskiego, E. I. Zastosowanie Wielokatow Czestotliwosci do selekcyi roslin. (Application of Frequency of Polygons in Plant Breeding.) Krakowie, 1909, pp. 1–32. Autoreferat in German, pp. 1–6.

ON SEX-CHROMOSOMES IN HERMAPHRODITISM

Researches by Boveri and his pupils have shown in certain nematodes, as in arthropods, the existence of two sorts of spermatozoa, one of which contains one more chromosome or chromosome

component than does the other. Eggs fertilized by the one sort of sperm develop into females, those fertilized by the other sort develop into males, as is shown by a cytological study of the two sexes, the female invariably containing the greater number of chromosomes or chromosome components.

Some results of especial interest have been obtained by Boveri[1] from studies of a little nematode (*Rhabditis nigrovenosa*) which occurs as a parasite in the lung of the frog. A free-living generation alternates with the parasitic one. It has long been known that the parasitic generation consists exclusively of females, but the free-living one of both sexes. According to Leuckart and Boveri, parthenogenesis may occur in the parasitic generation, though it is not the exclusive method of reproduction in this generation. For Anton Schneider, recently confirmed by Boveri, found spermatozoa in the genital tract of the parasitic female, and further established the remarkable fact that these spermatozoa develop in the ovarian tubules of the young female herself, which therefore, though a female in external form, is really a hermaphrodite. The close-fertilized eggs of the parasitic worm develop into embryos which are voided with the feces of the host and form the free-living generation, consisting of sexually separate males and females. These produce in turn, from fertilized eggs, the parasitic generation composed exclusively of hermaphroditic females.

The question which Boveri studied was this—how is sex determined in the parasitic generation? Are the spermatozoa of the self-fertilized mother dimorphic, and if so how do they arise?

First of all he established the fact that the spermatozoa found in the parasitic females are of two sorts. The chromosomes may be counted even in the mature sperm, and were found to be in part of the spermatozoa *six* in number, in part of them *five*. In the egg and polar cells were found always six elements. The fertilized egg therefore must contain either *twelve* or *eleven* chromosomes. From one of the former sort doubtless develops a female, from the latter a male. For in the male of the free-living generation Boveri found 11 chromosomes disposed as follows in the spermatocyte of the first order: 5 tetrads, 1 dyad (x chromosome), an arrangement explained as due to splitting of each of the 11 elements, ten of which were disposed in five pairs, forming

[1] "Ueber das verhalten der Geschlechtschromosomen bei hermaphroditismus," *Verh. d. phys.-med. Gesellschaft zu Würzburg*, N. F., 41, pp. 83–97, 1911.

in their split condition tetrad groups, the eleventh being the unpaired x element, as split a dyad. The x chromosome (dyad) passes entire into one of the spermatocytes of the second order, the end result being the formation of spermatids of two sorts, those which contain six and those which contain five chromosomes.

Now arises the first difficulty. If the male individual forms two sorts of spermatozoa, why are not offspring of *both sexes* produced by the free-living generation, instead of females alone? Boveri finds no evidence of degeneration in the spermatozoa containing only 5 chromosomes, and he finds that both sorts are received by the female at copulation, but assumes that the 5-chromosome sort is for some reason incapable of fertilizing the eggs, because from these develop only females containing 12 chromosomes. He relies here upon an analogy with the case of aphids and phylloxerans worked out by Morgan and von Baehr. In those cases, namely, the spermatids with the smaller number of chromosomes fail to develop. In the present case, though developed, they fail, in Boveri's opinion, to function in the fertilization of the egg.

Now comes the second difficulty. If the cells of the (hermaphroditic) female contain *twelve* chromosomes, how does she form spermatozoa containing *five* chromosomes, which is less than the *half-number?* Boveri finds that it is by a peculiar method of cell-division in spermatogenesis. In oogenesis there appear in the oocyte of the first order 6 tetrads which are distributed equally at the maturation divisions. The egg accordingly always contains 6 elements. But in spermatogenesis, in the same hermaphrodite generation, there form 5 tetrads and in place of the sixth a pair of separate dyads which are identified as x-elements. These lag behind the tetrads in division, so that when the five other elements have been distributed in cell-division these two remain at the equator of the spindle. Boveri was unable to ascertain just what does become of them but he assumes that one spermatid lacks them altogether, and this becomes the *male-determining* sperm. What Boveri failed to observe seems to have been observed by W. Schleip,[2] who finds that one x-element passes into half the spermatids, but the other remains on the spindle and does not enter a spermatid. Hence only half the spermatids contain six elements, the others contain five.

Why one process of reduction occurs in spermatogenesis and

[2] *Ber. d. Naturf. Gesell.*, Freiburg i. Br., 19, 1911.

another in oogenesis is unknown. Boveri makes several suggestions without adopting any of them as (1) position of the cells in the egg-tube, (2) seasonal conditions (sperm-production occurs first, egg-production later), (3) unequal plasmatic cell-divisions in the young worm, differentiating sperm-producing from egg-producing tissue.

As regards hermaphroditic animals in general, Boveri maintains that these, when they have the secondary characters of one sex only have that of the female rather than of the male, citing as examples gastropods and cirripeds. Females may retain the capacity to develop sperm, but males do not retain the capacity to develop eggs. For the male state is due to retrogressive variation, loss of cell-constituents, as for example of an x-chromosome. Now in the female this loss may occur *in certain reproductive cells only*, which then become reproductive cells of the male, *i. e.*, spermatozoa. But in the male individual, since *all* its cells are in the reduced state, reproductive bodies characteristic of the female (eggs) can not be produced. Nevertheless the male, though unable to form eggs (which we may assume can come only from a 2x cell) is able to form female-producing *gametes*, those with the full half number of chromosomes.

In its bearing on general theories of sex-determination Boveri's paper is important. It provides a way of reconciling the opposed views that sex-determination is independent of environmental influences and that it is dependent upon them. Both views are correct in part.

Sex is apparently in all cases controlled by cell structure, a clear index of which is afforded by the number of the chromosomes found in the nucleus. The more complete, or fully duplex, state is in all cases characteristic of the female; a more reduced state, either partially duplex or simplex, is characteristic of the male. But *external conditions* may influence the cell-constitution, and so indirectly determine sex. This is known to be the case in parthenogenesis and according to Boveri's observation in this paper it may be true in hermaphroditism also. Thus in rotifiers and daphnids abundant nutrition causes the unfertilized egg to develop without undergoing reduction, *i. e.,* in the fully duplex (2N) condition, and a female results; poor nutrition causes the unfertilized egg to delay development until maturation is complete and it has passed into the simplex condition, and a male results. The protoplasmic differences in the two cases are not confined to differences in chromosome number, the cell

size is also different, the female egg being larger. But the size-difference is not all-important, either, for the winter egg of the rotifers or daphnids is still larger, yet undergoes complete reduction, but will not develop in this condition unless fertilized; then it produces a female, being in the fully duplex, 2N condition. Sex in such cases is correlated with a particular cell-constitution, but this cell-constitution may be influenced by the environment; hence the environment may *indirectly* control sex.

Boveri's present contribution adds another important case to those previously on record. In the nematode, too, protoplasmic conditions control sex, but it is quite possible that external agencies as yet not identified may in this case also determine those protoplasmic conditions and so indirectly determine sex.

The question naturally arises whether the same may not be true in the higher animals also, those which are sexually separate. This idea has been strongly advocated from time immemorial, and still has its adherents, but a really critical analysis of the evidence shows that it rests on a very insufficient basis. In fact the experimental evidence is almost conclusive against it.

There is no *a priori* reason why the cell structure which differentiates male-producing from female-producing gametes or zygotes should not be controllable through environmental agencies in the higher animals, as in parthenogenetic animals. But *is* it? This is a question of fact, in determining which we must weigh evidence. The really critical examination of such evidence was begun in 1900 by Cuénot in a notable paper published in in the *Bulletin Scientifique,* and has been followed up by several others who have carried out carefully planned experimental researches, as, for example, Oscar Schultze. Their evidence is almost wholly against the idea that sex in the higher animals can be controlled either directly or indirectly. Russo,[3] indeed, still maintains this view. He holds that by feeding or injections of lecithin the structure of the ovule in the rabbit ovary may be altered, and that a female embryo develops from such altered ovules. Now there are two questions of fact involved in this evidence, first whether the cell-structure described by Russo is induced by the lecithin treatment or by some other agency. This is a question for cytologists to answer. The second question is whether the cell structure described has anything to do with sex-determination. This is a question in part for the experimental breeder to answer. From this point of view I have elsewhere

[3] *Biol. Centrbl.,* 1911.

discussed Russo's data. Two independent repetitions of his breeding experiments, one made in Italy, the other in England, have failed to confirm his conclusions, which therefore, as matters stand, have slight weight.

W. E. Castle.

Bussey Institution,
Harvard University,
June 12, 1911.

NOTES ON ICHTHYOLOGY

In the *Abhandlungen of the Akademie der Wissenschaften,* in Bavaria, Vol. IV, Münich, 1910, Victor Franz has an elaborate account of the bony fishes collected in Japan by Haberer and Döflein. This is an important paper, containing descriptions and figures of numerous new species.

In the Contributions from the Zoological Laboratory of Indiana University, No. 76, part 2, Dr. Carl H. Eigenmann gives a "Catalogue and Bibliography of the Fresh-water Fishes found in Tropical and South Temperate America," including all south of the latitude of the mouth of the Rio Grande. Dr. Eigenmann gives a discussion of the valid reasons which have led him to retain the generic name *Æquidens* in place of *Acara.*

In the *Bulletin of the Bureau of Fisheries,* Vol. XXIX, 1909, Jordan and Evermann discuss the "Salmonoid Fishes of the Great Lakes," with numerous plates, some of them in color. The name *Leucichthys* of Dybowski is adopted in place of the earlier name, *Argyrosomus,* of Agassiz, which was first used for a marine fish. Four new species of *Leucichthys* or lake herring are described, *L. supernas* from Lake Superior, *L. cyanopterus* from Lake Superior, *L. manitoulinus* from Lake Huron, and *L. ontariensis* from Lake Ontario. A new variety, *L. harengus arcturus,* is described from the west end of Lake Superior. Two new sub-generic names are adopted: *Thrissomimus* Gill for the ordinary lake herring, the name *Argyrosomus* being preoccupied; and *Cisco* for the deep-water forms. In this paper it is shown that the shore lake herring, instead of constituting a single species, are really several in number, at least six of them in the Great Lakes deserving recognition as species.

In the *Bulletin of the Bureau of Fisheries,* Vol. XXIX, 1909, Dr. Charles W. Greene discusses in detail the migration of the salmon in the Columbia River, treating with considerable fullness the methods by which individuals may be marked.

A number of tables are given illustrating the movement of the salmon, an average in the Lower Columbia being about seven and a half miles per day.

In the Bulletin of the Illinois State Laboratory of Natural History, Dr. Stephen A. Forbes gives a table and a series of maps illustrating the distribution of the different species of fishes, as traced in the state of Illinois. One hundred and fifty native species are recognized, all of them represented in the neighboring states, variously extending into the rather monotonous basin of Illinois, in accordance with the character of the water. In the absence of geographical barriers, the causes influencing their distribution are climatic, geologic and ecological. A number of other generalizations are developed.

The British Museum of Natural History has issued the second volume of George A. Boulenger's important "Catalogue of the Fresh-water Fishes of Africa." This covers the catfishes, and a portion of the carp family. Most of the species are illustrated by good drawings.

In the *Annales de L'Institut Oceanographique,* of Prince Albert of Monaco, Dr. Louis Fage gives an account of the many forms of larval fishes taken in the deep-sea work of the Prince of Monaco.

In the *Philippine Journal of Science,* Vol. V, July, 1910, Mr. Alvin Seale describes four new species of fishes from Bantayan Island.

In the *Memoirs of the Indian Museum in Calcutta,* Vol. III, 1910, Dr. N. Annandale and J. T. Jenkins describe and figure numerous fishes taken in deep water by the steamer "Golden Crown."

In the *Memoirs of the Museum of Comparative Zoology,* at Harvard University, Vol. XXVI, 1911, William C. Kendall and Edmund L. Goldsborough record the species of shore-fishes taken by the *Albatross* in the South Seas, when in charge of Professor Alexander Agassiz. Numerous new species are described, and valuable notes are given on those recorded by previous authors.

In the *Proceedings of the United States National Museum,* Vol. 38, 1910, Jordan and Thompson discuss the "Gold-eye of Lake Winnipeg," an excellent food fish which has been generally overlooked by authors, *Amphiodon alosoides.*

In the same *Proceedings,* Vol. 39, 1911, Jordan and Thompson discuss the "Fishes of the Families *Lobotidæ* and *Lutianidæ,*" found in the waters of Japan.

In the same *Proceedings,* Vol. 39, 1911, the same authors discuss the species of the family *Sciænidæ* found in the waters of Japan.

In the same *Proceedings,* Vol. 38, 1910, Barton A. Bean and Alfred C. Weed discuss the "Venomous Toadfishes of South America" belonging to *Thalassophryne* and related genera, with figures of the different species and a discussion of the venomous spines by which they are armed.

In the same *Proceedings,* Vol. 39, 1911, Theodore Gill discusses the "Structure and Habits of the Wolffishes." The genus *Lycichthys,* based on *Anarrhicas latifrons,* is here fully defined. A new species, *Lycichthys fortidens,* from the North Atlantic, is described and figured.

In the same *Proceedings,* Vol. 38, 1910, William Converse Kendall describes a collection of fishes made in Labrador by Owen Bryant. Among these are certain sea trout not belonging to the ordinary brook-trout species, *Salvelinus fortinalis.* The species in question is provisionally identified as *Salvelinus stagnalis,* but it is possible that it is a species still undescribed. The name *Salmo immaculatus* was probably originally given to this species, but the name is preoccupied.

In the same *Proceedings,* Vol. 38, 1910, Barton W. Evermann and William C. Kendall compare the chub-mackerels, *Scomber colias,* of the Atlantic, with those of the Pacific, called *S. japonicus.* They find the two species different, in measuring the specimens examined, the head being especially larger in the Pacific fish—about $3\frac{1}{4}$ instead of $3\frac{2}{3}$ in the length of the body. Comparison of other specimens made at Stanford University does not seem to bear out these differences, and the propriety of separating the Atlantic species from the earlier named Japanese form as *Scomber colias* is still doubtful.

In the same *Proceedings,* Vol. 37, 1910, Barton A. Bean and Alfred C. Weed discuss the Japanese genus *Anteliochimæra,* in which they show that the genus is probably identical with *Harriotta,* an Atlantic genus of *Chimæra.*

In the same *Proceedings,* Vol. 39, 1910, Barton W. Evermann and Homer B. Latimer give a "Catalogue of the Fishes," forty in number, known to inhabit the Lake of the Woods.

In the *Annals and Magazine of Natural History,* November, 1910, C. Tate Regan discusses the families of Zeidæ and Caproidæ.

In the same *Annals* Mr. Regan discusses the origin and evolution of the order of the flounders. He regards them as descended

from perchlike fishes—the genus *Psettodes* with a spinous dorsal, being the most primitive of the group. He divides the flatfishes into four families, Bothidæ, Pleuronectidæ, Soleidæ and Cynoglossidæ. He finds no evidence that the flounders are related to *Zeus,* as suggested by Boulenger. The relation to the fossil genus *Amphistium* seems to be possible. In Regan's judgment this fish is a percoid, allied to *Psettus* or to *Platax.* The adjustment of the genera of flounders is somewhat different from that usually accepted.

In the *Proceedings of the Biological Society of Washington,* Professor T. D. A. Cockerell discusses the scales of various soft-rayed fishes. He finds in the structure of the scale valuable characters for the distinction of genera and subgenera, in different groups of fishes. This is the first critical study of scales with a view to using their characters in the classification of genera, and Mr. Cockerell's observation should be extended throughout ichthyology.

In the *Bulletin of the American Museum of Natural History,* Vol. XXVIII, 1910, John Treadwell Nichols discusses the occurrence of the pelagic pipefish, *Siphostoma pelagicum.* They occur especially in the drifting Gulf weed of the mid-ocean. Mr. Nichols has also examined the type of *Caranx forsteri* from the Ile de France. He considers that this species is identical with the *marginatus* of Gill; the *rhabdotus* of Jenkins; and the *elacate* of Jordan and Evermann. The specimen called *forsteri* in Jordan and Evermann's Hawaiian report, he thinks identical with the Atlantic species *latus.*

In the *Bulletin of the American Museum of Natural History,* Vol. 28, John T. Nichols describes two new blennies from Florida, *Stathmonotus tekla* from Key West, and *Blennius fabbri* from Miami.

In the *Annals and Magazine of Natural History,* 1910, Holt and Byrne describe a new deep-water fish as *Grammatostomias flagellibarba.*

In the *Bulletin of the American Museum of Natural History,* Vol. XXVIII, 1910, Russell J. Coles describes an interesting collection of fishes from Beaufort, N. C. One of these is *Mobula olfersi,* the small devil fish. Several other rare West Indian species are recorded by Mr. Coles.

In the AMERICAN NATURALIST, 1909, E. W. Gudger records a number of species of interesting fishes found also at Beaufort.

In the *Proceedings of the Royal Society of Queensland,* 1910,

Mr. J. Douglas Ogilby describes a number of new species of fishes from the neighborhood of Brisbane.

In the *Notes from the Leyden Museum*, Vol. XXXII, Professor Max Weber describes a number of new species of fishes from New Guinea.

In the *Revista do Museu Paulista*, Vol. VIII, 1910, Professor Rodolpho von Ihering describes a number of new catfishes from the neighborhood of São Paulo, in Brazil.

In the *Bulletin of the American Museum of Natural History*, Vol. XXX, 1911, Dr. Charles H. Gilbert describes a number of lantern fishes. One of them, *Lampanyctus nicholsi*, is new, taken near the Falkland Islands.

In *Science*, Vol. XXXI, Dr. George Wagner, of the University of Wisconsin, describes a new Cisco, from Lake Michigan, under the name of *Argyrosomus johannæ*. Of this species a colored figure is given by Jordan and Evermann in the article noticed above.

In the *Annals of Scottish Natural History*, January, 1911, Mr. C. Tate Regan discusses the giant pike of Loch Ken, in Scotland, which reaches a weight of over seventy pounds.

In the *Annals and Magazine of Natural History*, Vol. VII, Mr. Regan discusses the "Systematic Position of the Genus *Macristium*." *M. chavesi* is a deep-water fish which represents a family related to *Alepocephalus*.

In the same *Annals*, Vol. VIII, Mr. Regan discusses the "Lampreys of the World." He regards *Bathymyzon* as an ordinary lamprey with the teeth feeble. In *Ichthyomyzon* he recognizes two species, *bdellium* and *castaneus*, rejecting the name *concolor* as being based on a larva, perhaps of *Lampetra*. The species, *spadiceus, japonicus* and *wilderi* are referred to the genus *Entosphenus* instead of *Lampetra*.

In the *Annals of the Carnegie Museum*, Vol. VII, 1910, Dr. Jordan describes a series of fossil fishes belonging to the Carnegie Museum, and obtained by Dr. John C. Branner in Brazil. These fishes are from Eocene rocks at Riacho Doce in Brazil. Two new genera are described, *Ellipes* and *Dastilbe*, both of these being based on diminutive herring.

In the *Transactions of the New Zealand Institute*, Vol. XLII, 1909, Edgar R. Waite gives a "Catalogue of Fishes from Kermadec and Norfolk Islands."

In another paper in the same *Annals* he gives notes on various New Zealand fishes.

In the *Annals of the Carnegie Museum*, Vol. VII, Jordan and

Thompson describe a collection of fishes made by Professor J. F. Abbott at Irkutsk in Siberia. Several figures of rare species are given.

In the *Proceedings of the Biological Society of Washington,* William C. Kendall shows that the trout-perch should be called *Percopsis omiscomaycus.* The forgotten name of Walbaum (*Salmo omiscomaycus*) clearly belongs to this curious fish.

In the "Fortieth Annual Report of the Fisheries of Rhode Island," Dr. Henry C. Tracy gives a list of the fishes known to inhabit that state. Among these are several rare forms from the West Indies.

In *Science,* Vol. XXXII, George Wagner discusses the stickleback of Lake Superior, and shows that *Eucalia pygmœa* from Lake Superior is not distinct from the ordinary *Eucalia inconstans.*

In the *Bulletin of the American Museum of Natural History,* Vol. XXIII, 1907, Newton Miller describes the fishes of the Montagua River in Guatemala. The following new species are recorded: *Pœcilia amates, Thyrina meeki, Cichlasoma spilurum, Cichlasoma globosum, Cichlasoma mañana, Cichlasoma acutum.*

In the *Arkiv for Zoologie* Band 4, Ribeiro describes some catfishes from the Iporanga River, near São Paulo in Brazil.

In the *Proceedings of the Biological Society of Washington,* Barton W. Evermann and T. D. A. Cockerell describe three new species of minnows, *Richardsonius thermophilus* from Warm Springs, Ore.; *Notropis kendalli* from Cross Lake Thoroughfare, Me.; and *Notropis universitatis* from Boulder, Col.

In the same *Proceedings,* Mr. Cockerell and Mr. Otis Callaway describe the scales of various minnows of the United States. A subgenus, *Coccogenia,* is established for *Notropis coccogenis.*

In the *Annals and Magazine of Natural History,* Vol. VII, 1911, Mr. Regan discusses the families of Berycidæ and their relationship. He proposes to regard the Berycomorphi as forming a distinct order, and a second order, *Xenoberyces,* is established for the Stephanoberycidæ, Melamphaidæ and other relatives.

In the *Proceedings of the United States National Museum,* Vol. 38, 1910, Professor E. C. Starks and W. F. Thompson review the flounders of the genus *Pleuronichthys,* with two new species, *P. nephelus* from San Juan Islands, Puget Sound, and *P. ocellatus* from the Gulf of California.

In the *Annals and Magazine of Natural History,* Vol. VII, 1911, Mr. Regan discusses the "Anatomy and Classification of the Teleostean Fishes of the Order Iniomi," bringing the various

groups into clearer relations with each other. He places the genus *Ateleopus* among the Iniomi.

In the *Philippine Journal of Science,* Vol. V, 1910, Alvin Seale describes a collection of fishes from Borneo.

In the *Proceedings of the Academy of Natural Sciences of Philadelphia,* April, 1910, Henry W. Fowler describes and figures the types of many species of American fishes of the genus *Notropis.*

In the same *Proceedings,* Mr. Fowler describes *Paralepis barracudina,* a new species from Corson's Inlet, New Jersey.

In the same *Proceedings,* Mr. Fowler describes various little-known fishes from New Jersey, and also a number of new species of ganoid fishes. He divides the garpikes into two genera, *Lepisosteus* and *Cylindrosteus.* Instead of the three species usually recognized, Mr. Fowler discussed twelve. It has been evident for some time that the number of species in this group is much greater than the three admitted by Jordan and Evermann. The value of the different species defined by Mr. Fowler, however, is yet to be proved. It will be necessary to have a very large amount of material before these questions of identity can be fully decided.

The species recognized by Mr. Fowler are: *Lepisosteus huronensis, L. osseus, L. treculii, L. clintonii, Cylindrosteus platostomus, C. scabriceps, C. productus, C. agassizii, C. castelnaudii, C. megalops, C. tristœchus, C. tropicus.*

In the same *Proceedings,* Mr. Fowler describes *Dixonina nemoptera,* a new species of albuloid from Santa Domingo. This genus differs from Albula in having the last ray of the dorsal and anal filamentous.

In the *Proceedings of the National Museum,* Vol. 40, 1911, W. C. Kendall describes two very rare species of sole, *Gymnachirus fasciatus,* from Long Key, Fla., and *G. nudus* from Tisbury Great Pond, on Marthas Vineyard. Both are doubtless strays from the Gulf Stream.

In the *Bulletin of the University of California,* Geology, Vol. V, James Z. Gilbert describes a fossil flounder, *Evesthes jordani,* notable for its large mouth, from Miocene rocks near Lompoc, in California. This is one of the oldest-known of fossil flounders, and its relations are evidently with the halibut tribe, and with the genera still represented on the California coast.

In *Science,* Vol. 30, H. H. Newman shows clearly that the killifish *Fundulus majalis* is never viviparous.

In the *Proceedings of the United States National Museum* for

1911, Barton A. Bean and Alfred C. Weed discuss the habits of the electric ray, *Narcine brasiliensis.*

In the same *Proceedings,* for 1911, Dr. Hugh M. Smith and Lewis Radcliffe describe three new species of butterfly fishes from the Philippines.

In the *Mémoires de l'Académie Royale des Sciences et des Lettres de Danemark,* Dr. Hector F. E. Jungersen describes in great detail the anatomy of the pipefishes and trumpet fishes, and their relatives. In this, numerous errors of interpretation made by different authors are corrected, and the paper is one of high merit.

In the *Annals and Magazine of Natural History,* Vol. VII, 1911, Mr. C. Tate Regan discusses the fishes related to the silver gar and flying fish, in the order of Synentognathi. He recognizes two suborders, the one containing the families of Belonidæ and Scomberesodinæ, the other containing the Hemirhamphinæ and Exocœtidæ. He suggests the close relation or possible identity of the fossil genus *Cobitopsis* with *Chriodorus.* Regan regards *Esox lucius,* the supposed *Esox* of Pliny, as the type of *Esox.* He retains *Belone* for the European silver gar, rejecting *Ramphistoma* as a nomen nudum.

In the same *Annals,* Mr. Regan describes the new order Microcyprini, containing the Amblyopsidæ and the Pœciliidæ, each of which families represents with him a distinct suborder. This leaves in the order of Haplomi only three families, the Esocidæ, Umbridæ and Dalliidæ. He thinks that the Haplomi are related to the isospondylous fishes, while the Microcyprini are nearer to the Synentognathi. Mr. Regan notes that the genera *Retropinna, Microstoma* and *Salanx* lack the mesocoracoid characteristics of the other salmon-like fishes. Nevertheless, he regards these along with the fresh-water trout-like fishes of the southern hemisphere, the Galaxiidæ and the Haplochitonidæ, as true Salmonoids, although these latter have also lost the mesocoracoid. The fossil family of Enchodontidæ, Regan regards as an ally of the Stomiatidæ. The Kneriidæ he regards as near to the *Chanidæ.* Regan regards *Panchax* as a genus distinct from *Aplocheilus. Aplocheilus* originally contained two distinct types, but the name was definitely restricted by Bleeker to the group having no vomerine teeth. *Oryzias,* which belongs to the latter group, Regan regards as a synonym of *Haplochilus.* Apparently the short jaws of *Oryzias* should distinguish it from *Aplocheilus,* though it may be identical with some of the African genera.

In the same *Annals,* Mr. Regan discusses the order of Salmo-

percæ. Beside *Percopsis* and *Columbia,* he adds to this group a genus *Aphredoderus,* this form without an adipose fin constituting a distinct family. He notes that the study of the anatomy of the last genus does not indicate any real affinity with the sunfishes.

In the same *Annals,* Mr. Regan discusses the allies of the genus Cirrhites. In this group he finds five distinct families.

Over thirty years ago, when the great house of Godeffroy, of Hamburg, was dominating the trade of the South Seas, this company undertook the establishment of a natural history museum in Hamburg, and with this the publication of a journal called the *Journal des Museum Godeffroy,* in which the life of the South Seas should be set forth. This journal was sumptuously printed, and illustrated with expensive colored plates. One of the important articles was that descriptive of Andrew Garrett's Fische der Südsee, Andrew Garrett having made an extensive collection of fishes in various islands, and having made colored paintings of a large number of the species. During the time, 1876–1881, the first two volumes of the Fische der Südsee appeared, the author being Dr. Albert Gunther, keeper of the British Museum. The work ended abruptly in the middle of the family of *Labridæ.* The great house of Godeffroy, having undertaken in Europe enterprises beyond its control, went into collapse, and the publication of its journal was suspended. In 1909, under the management of Friedrichsen & Company (publishers), the work has been resumed and brought to completion, with the assistance of Mr. C. Tate Regan, of the British Museum. This has been made possible by the "munificence of the family of Dr. Wilhelm Martin von Godeffroy."

This completed work is a monument to the industry and keen intelligence of Dr. Gunther, and it is the most important treatise concerning the fishes of the region between Hawaii and Borneo known as the South Seas. In the different papers by Jordan and Evermann, and their associates, Snyder, Fowler and Seale, much of the same ground has been covered, and Dr. Günther gives special credit to "the energy" of these American authors in their investigations, particularly of the Hawaiian and Samoan archipelagos. Comparing this work with Jordan & Seale's "Fishes of Samoa," we find a general agreement on all matters where adequate material is present. The American writers generally have given proposed new species the benefit of doubt, by not reducing them to synonymy until it is shown that the new name is a mere synonym. On the other hand, Dr. Günther has

consistently left new species in synonymy unless their right to independent rank has been made clear. In general, the British Museum publications have been characterized by the assumption that a species is not valid until it is represented in the collections of the museum. There is room for many differences of opinion in regard to the relation of certain forms, and in regard to matters of nomenclature, but there can be no difference of opinion as to the great value of this work, and as to the accuracy of these fine plates, most of these being copies of the colored drawings of Mr. Garrett.

In the *Zoological Magazine* of Tokyo, Dr. Kishinouye has a paper on the Sparoid fishes of Japan. It is probably a valuable paper, but, being written almost entirely in Japanese, it becomes inaccessible to naturalists of the rest of the world, and it is hoped that this will not establish a precedent, at least unless a résumé in some modern language can accompany the descriptions of new species, and the new material which the writer is able to add.

David Starr Jordan.

Stanford University.

SOME RECENT BOOKS ON FOSSIL PLANTS

The appearance within two years of three general works on paleobotany, is a sufficiently marked indication of the great interest which this phase of botany at the present time is exciting in England.[1] Much of the most important work which is now being published by the British botanists deals with fossil plants.

The English botanist is in some respects at a great disadvantage compared with his American colleagues. The comparatively meagre flora of the British Islands has already been exhaustively studied, and is a strong contrast to the extensive and varied flora of North America, which, except in the older parts of the country, still offers a rich field to the systematist and plant-geographer, as well as to students of morphology and physiology. This difference in the natural advantages of the two countries no doubt explains to some extent the greater interest in fossil plants shown by the English botanists. But unquestionably much more important is the availability of great collections of important fossils awaiting investigation; and the important

[1] Scott, D. H., "Studies in Fossil Botany," 2 vols., London, Adam and Charles Black, 1908–9. Seward, A. C., "Fossil Plants," Vol. II, Cambridge University Press, 1910. Stopes, Marie C., "Ancient Plants," Blackie & Son, London, 1910.

results already obtained by workers in this field offer great inducements to the young botanist. It must not be inferred that no interest is shown in the study of fossil plants by American workers, but paleobotany has not received the same attention here as in England.[2]

The many important contributions to the study of fossil plants by Scott and Seward are familiar to all students of paleobotany, and their treatises have the stamp of authority. Miss Stopes has published papers of much value, and her little volume presents in clear and fairly untechnical language some of the most important topics of the science. While the books of Professors Scott and Seward are designed primarily for botanical students, and are necessarily technical in their treatment, Miss Stopes's volume is intended mainly for the layman, and seems well suited to its purpose.

Professor Scott's two volumes deal almost entirely with the vascular plants, especially the Pteridophytes, which, as might be expected from the author's intimate knowledge of these forms, are handled in a thoroughly adequate fashion. The first volume treats of the Pteridophytes proper, while the second deals with the seed-bearing forms, including a very full and satisfactory treatment of those seed-bearing ferns, the "Pteridosperms" or "Cycadofilices," the investigations of which during the last ten or fifteen years have made such profound changes in our conceptions of the nature of the fern-like plants of the Paleozoic.

The Cycads and their fossil relations, the Benettiteæ, or Cycadeoideæ, are also treated at length, and the Cordaitales receive ample treatment; but the Conifers are passed over very briefly, and no account at all is given of the fossil Angiosperms, a group which is in woeful need of careful treatment by competent investigators.

Professor Seward's work is on a somewhat larger scale, and takes into account the whole vegetable kingdom. The work is, however, incomplete as yet. The present volume, the second of a proposed series of three, is devoted mainly to the Lycopods and ferns. The former volume comprised the Thallophytes and Bryophytes, together with the most of the Equisetineæ. The third and concluding volumes proposes to deal with the seed-bearing plants, including the Pteridosperms.

[2] In Coulter and Chamberlain's recent valuable treatise on the Gymnosperms, the fossil forms are treated at length, and this section of the book is one of its most valuable features. The important work of Wieland, Jeffry and other students of fossil plants in America must not be overlooked.

With these three books, at the same time reliable in their statements, and attractively written, English and American students can have no excuse for ignorance of the present status of paleobotany.

The attitude of botanists toward the study of fossil plants has undergone a marked change of late years. It is now no longer true that the students of fossil plants know little or nothing about living ones, and the great advancements of late years are largely due to the fact that recent students of fossil plants are thoroughly trained botanists. Moreover, as in other branches of botany, greatly improved methods have been developed, and the microscopic study of sections of petrified plant-tissues now make it possible in many cases to examine accurately the tissues of the fossil plants, and to compare them with the living forms supposed to be related to them. The perfection of some of these sections of fossil tissues is quite astonishing.

Of course it is the firmer tissues, like the epidermis and woody structures of the vascular plants which are most commonly preserved, and it is not strange that the paleobotanist should lay great stress upon the importance of the vascular skeleton which is so perfectly preserved. Students of living plants sometimes think that the great morphological importance attributed to the vascular system has been rather exaggerated, and there is no question that some of the far-reaching conclusions drawn from what to the layman seems very inadequate evidence, are not justified when they are taken in connection with the evidence furnished by a study of living forms. One can not accept without reserve many of the conclusions drawn from the study of fragmentary material, often very badly preserved. Nevertheless, no one can dispute that great advances have been made in our knowledge of the history of the development of the plant kingdom resulting from the discoveries made by students of fossil plants.

The problems which confront the student of fossil plants, and the difficulties which he encounters, are well set forth in the introductory chapter of Dr. Scott's book. The extremely fragmentary character of the record, and especially the great difference shown by different periods in the preservation of plant remains, are clearly set forth. The Carboniferous, as the students of fossil plants are aware, affords the richest fossil flora known, and it is especially with the Carboniferous flora that Dr. Scott concerns himself.

As it is among the Paleozoic Pteridophytes that we are to

look for the ancestors of the modern seed-bearing plants, the rich pteridophytic flora of the Carboniferous naturally takes first place, and it can be readily understood that an absorption in the study of these interesting fossils should perhaps overshadow the importance of other forms. One can not help feeling that if the search for remains of the Bryophytes in the Paleozoic rocks had been pursued with the same zeal as has been shown in the study of the vascular plants, something more than the extremely fragmentary evidences of their existence would be forthcoming.

Professor Seward, in his first volume published in 1898, has given an admirable account of the different methods of fossilization, and also the distribution of fossils. He points out in a very interesting and convincing way the evidences of the existence of the same factors at work at the present day as in times past. Perhaps the most striking fact brought out in the distribution of plant remains is the at first puzzling occurrence of freshwater and land plants in deposits of evident marine origin. Professor Seward, however, shows that the great rivers of to-day, like the Amazon and the Mississippi, are carrying out to sea rafts of vegetation which may very well at some distant time be discovered as fossils covered by marine deposits, to puzzle the geologists of that future epoch.

The history of the fossil Thallophytes remains very much as it was at the time Professor Seward's first volume was published, a rather significant comment on the neglect of these important plants when compared with the great advances made in our knowledge of the fossil Pteridophytes and Gymnosperms during the past decade.

As most of the Thallophytes, especially the algæ, are extremely delicate and perishable organisms, the rarity of recognizable fossil remains is not to be wondered at. Where there is a calcareous incrustation, as in the coralline algæ and many Siphoneæ, very perfect fossils have been preserved. The latter group is especially well represented in a fossil state and has received considerable attention from the paleobotanists. Some of these Siphoneæ can be traced back to the Silurian, and the order is evidently a very old one. A study of these algæ shows that, as at the present day, they played a by no means unimportant rôle as reef-builders.

Among the most characteristic of fossil plants are the Diatoms. While these have left enormous deposits of their flinty shells in the Cretaceous and later rocks, they are practically unknown in

the earlier formations. It is highly probable that in spite of their simple structure the Diatoms are really comparatively recent types. Their enormous numbers and practically universal distribution at the present time, indicate that they are admirably adapted to existing conditions. They particularly abound in the Arctic and Antarctic seas.

While the Fungi are rarely preserved in a very satisfactory condition, there is abundant evidence of their presence in the Paleozoic rocks.

The geological history of the Bryophytes is in a very unsatisfactory condition. Of the liverworts only a few impressions are recorded, and these, according to Seward, are all from Mesozoic or Tertiary formations, and so closely resemble the living species that they throw no light upon the early history of the group. Very few fossil remains which can with certainty be referred to the true mosses are known, but the possibility of confusing the remains of mosses with small Lycopods or even fragments of coniferous branches has to be taken into account.

It has been suggested that the very small number of unmistakable Bryophytes which has been recorded in a fossil state might be explained in the same way as we have suggested for the absence from the Paleozoic rocks of Diatoms; but the cases are hardly parallel since the Bryophytes, particularly the liverworts, give every evidence of being old and generalized types, and do not appear to be particularly well adapted to modern conditions, except as these duplicate what we may assume to have been the conditions during the Carboniferous. It is only in the extremely moist, even climate of the mountain tropics, where the other Paleozoic type, the Pteridophytes reaches its greatest luxuriance, that the liverworts form a conspicuous feature of the flora. Moreover, the liverworts are far less plastic, the number of species, even of wide-spread genera (except in the leafy forms) being usually very small. Both their distribution and their structures point unmistakably to their being a primitive group.

The absence of liverworts from the early geological formations can most readily be explained on the score of their great delicacy, which would prevent their being preserved in a recognizable form. Even were we to admit that the liverworts are modern types, we should still have to explain why their progenitors, and the presumably similar progenitors of the ferns, have not been found in a fossil condition. A parallel case is found in the Cretaceous and Tertiary formations, where the great deposits

of perfectly preserved plant remains are almost entirely referable to trees and shrubs, while the host of herbaceous plants, like the grasses and delicate herbs forming the carpet of the forests, are conspicuous by their absence. If magnolias and maples were abundantly developed in the Tertiary forest, we may be sure that there were also buttercups and violets, although we have no impressions of their leaves and flowers. The same explanation for the extreme scarcity of impressions of herbaceous plants in the Cretaceous and Tertiary formations may be applied to the much more delicate hepatic flora of the Paleozoic.

In the light of comparative morphology, we think most botanists will agree that it is in the highest degree probable that the simpler liverworts, like *Aneura* and *Pellia,* are extremely ancient types, which, like the majority of the algæ, owing to their very delicate and perishable tissues, simply have failed to leave recognizable fossil traces. The only structures of the liverworts which one might hope to recognize in a fossil state are the elaters. It may be that a careful examination of sections of the masses of petrified vegetation resulting from the débris of the Carboniferous forests, may show liverwort elaters, but as yet no such discovery has been recorded. It is also by no means impossible that among the numerous beautifully preserved leaf impressions of the Paleozoic ferns, some might under specially favorable conditions show traces of epiphyllous liverworts, such as are common on fern leaves at the present day in wet tropical forests.

It is the Pteridophytes and their allies among the simpler seed-bearing plants that have largely monopolized the attention of the paleobotanists during the past decade or two. The results of these investigations have been to quite readjust the views long held as to the real nature of many of the Paleozoic fossils. These changes have been mainly among the fern-types, although among the Equisetineæ and Lycopods there have also been important discoveries.

The history of the fossil Equisetineæ need not be dwelt upon here. It is sufficiently well known that this class, at the present day reduced to some twenty-five species belonging to the single genus *Equisetum,* was an important factor in the rich Paleozoic flora. Professor Scott, in the first volume of his studies, gives an excellent account of the present status of our knowledge of this class.

The Lycopods, also a comparatively degenerate group at the present day, showed much greater range of structure and size than at present. The most important discovery of late years

among the fossil Lycopods is the fact that some of the great fossil club-mosses, *e. g., Lepidocarpon,* bore unmistakable seeds. This adds one more instance of the independent origin of seeds in quite unrelated orders of Pteridophytes.

It is among the ferns, however, that the interest of the paleobotanist has been especially centered, both in England and on the continent. The abundance and perfection of the fern-like fossils of the Paleozoic, especially those of the Carboniferous, are sufficiently familiar, but a very large percentage of them are merely impressions of sterile fronds. Numerous investigations of these supposed fern-leaves have proved beyond question that they are not ferns in the strict sense of the word, but are the sterile leaves of fern-like plants which bore true seeds. It has become apparent that these seed-bearing ferns, "Pteridosperms," formed a very important feature of the Carboniferous flora, perhaps outnumbering the true ferns. Indeed, some enthusiastic students of these interesting plants have gone so far as to doubt whether true ferns existed at all at this period!—a conclusion with which it is needless to say few botanists would be inclined to agree. True ferns must have preceded Pteridosperms, and it is hardly likely that none of them should have left fossil remains, not to mention the fact that many of the fossil fronds bear sporangia of whose true fern nature there can be no reasonable doubt.

Of the living ferns, the Marattiaceæ are best represented among the Paleozoic fossils, and their primitive nature is also shown by a study of their structure and development. Most of the Pteridosperms were probably derived from ferns of this type, and it is in many cases apparently not possible to decide whether certain leaves bearing sporangia of the Marattiaceous type are true ferns, or whether they represent the microsporangia of some Pteridosperms. It does not follow, however, as some students of Pteridosperms have argued, that because the sporangia of one doubtful Marattiaceous fern have been shown to belong to a Pteridosperm, that therefore we must suspect all of the sporangia of the Marattiaceous type.

The geological history of the other living family of the eusporangiate ferns, the Ophioglossaceæ, is extremely unsatisfactory. The great rarity of recognizable fossils belonging to this family may perhaps be explained by the perishable nature of their leaves. The soft leaves of *Ophioglossum* and *Botrychium* and the absence of indurated cells from the sporangium would make these plants very poorly fitted for preservation in a fossil state.

It is, however, by no means impossible that some of the earliest known ferns, the Botryopterideæ, may have been related to the Ophioglossaceæ. Both the form of the leaves, and the sporangia which were borne on special leaf segments, are suggestive of the Ophioglossaceæ, and there are also certain anatomical resemblances.

One of the earliest fern-like fossils is the Devonian genus *Archæopteris.* This fossil in the venation of the leaves suggests the simpler types of *Botrychium,* and the sporangia are borne on special leaf segments, which, however, it must be said more nearly resemble *Osmunda* than they do *Botrychium.* Professor Seward is inclined to believe that the sporangia of *Archæopteris* are really pollen-sacs of a Pteridosperm, stating that they are much larger than the sporangia of any known fern, being two or three mm. in length. It is evident that Professor Seward overlooked the Ophioglossaceæ in making this comparison, and it is with these that the comparison really should be made. The sporangia of *Archæopteris* are described as pear-shaped sacs, two to three mm. in length. These are nearly equalled in size by some species of *Botrychium,* such as *B. Lunaria* and *B. silaifolium,* in which the globular sporangia may be 1.5 mm. in diameter, while the sporangia of the large species of *Ophioglossum* very much exceed in size these figures. In *O. pendulum* the sporangia are probably larger than those of any other living Pteridophyte, and may reach a diameter of four millimeters. It is clear then that the mere question of size is not a valid argument for considering *Archæopteris* a Pteridosperm rather than a homosporous fern.

The evidence of the fossil record entirely bears out the conclusions based upon a study of the living ferns that the condition in which the sporophyll, or parts of it, are entirely devoted to spore-production, as in *Ophioglossum* and *Osmunda,* is a more primitive condition than that in which the sporangia are produced upon the backs of unmodified leaves.

There is abundant evidence from a study of existing Archegoniates that the sporophyte of the fern is the result of the elaboration of the sporogonium of some bryophytic ancestor. This being the case, it necessarily follows that the sporophylls are older phylogenetically than the sterile leaves, and are not secondary modifications of the latter. It is to be hoped that students of the Botryopterideæ and other archaic fern types will make a thorough comparison of these with the existing Ophioglossaceæ, in the light of the most recent developmental studies

on the latter. Whether or not we admit the relationship of *Ophioglossum* with these ancient ferns, there is no question that both in regard to the early history of the sporophyte and in the structures of the adult sporophyte, *Ophioglossum* most nearly represents among living ferns what we may fairly assume to have been the primitive type from which the higher ferns have sprung.

In view of the abundant evidence of the primitive nature shown by the living Ophioglossaceæ, we can not believe that these plants did not exist in the earlier geological epochs; and the failure to record them is due either to the complete disorganization of their delicate tissues, or to a failure by investigators to recognize the ferns allied to them which may have been found in a fossil state.

Dr. Scott in his second volume gives an excellent account of the Cordaitales and the Cycads, but it is to be regretted that his treatment of the Conifers is so brief. He explains this by stating that the present knowledge of the fossil Conifers is not sufficiently exact to make a satisfactory general treatment feasible. It is to be hoped that in the concluding part of Professor Seward's treatise they will receive adequate attention.

The Cordaitales, the earliest known seed plants and completely extinct at the present time, are remarkable for the perfection with which their floral structures, as well as their vegetative tissues, have been preserved. They evidently represent a more or less synthetic type with apparent connections with several of the other great groups, but their exact place in the system is still not quite satisfactorily settled.

The advance in our knowledge of the "Cycadophytes"—the Cycads and their relations—during the past ten years has been very great, largely due to the labors of an American paleobotanist, Dr. Wieland.[3] His remarkable studies on the wonderfully preserved Mesozoic Cycads of the Black Hills Region of South Dakota and Wyoming, form one of the most notable contributions to fossil botany that have been made for many years. These Mesozoic Cycads are separated from the recent type of Cycads as a distinct family, the Benettiteæ or Cycadeoideæ. It is the floral structures of these plants that have attracted the greatest attention, as they show a curious similarity in their general structure to such a flower as a magnolia, although they are gymnosperms. This resemblance is so striking that some stu-

[3] Wieland, G. R., "American Fossil Cycads," Carnegie Institution of Washington, Publication No. 34, 1906.

dents have even gone so far as to assume an origin for the lower Angiosperms from some similar type. Much more evidence, however, is necessary before so startling a theory can be accepted.

Professor Scott gives only a brief summary of the fossil history of the Conifers. The order can be traced back to the Permian and it is possible that some types are still older. The oldest recognizable Conifers were apparently allied to the modern Araucarias, and it may be noted in this connection that Seward has expressed the opinion that the Araucariaceæ show sufficient similarity to the Lycopods to warrant the hypothesis that they may have descended from some of the great seed-bearing Lycopods of the Carboniferous. True Araucariaceæ occur from the Triassic, and probably existed in still older formations.

The Taxodineæ to which our bald cypress and Sequoia belong, may go back to the Permian, but there seems to be some doubt of the real relationships of the earliest fossils placed in this family. The Abietineæ, *i. e.*, the pines and firs, do not occur before the later Jurassic and early Cretaceous formations, and the true cypresses seem to be of about similar age. The Taxaceæ, the Yew family, is apparently the most recent of the Conifers, not being found below the Cretaceous.

The geological history of the Angiosperms is very incomplete, and they have received very much less attention than the Pteridophytes and Gymnosperms which have so largely monopolized the attention of the paleobotanist. It would seem as if a critical investigation of the abundant Cretaceous and Tertiary remains of the Angiosperms, comparable to the many complete studies on the Paleozoic and Mesozoic Pteridophytes and Gymnosperms, should yield results which would throw some light upon the origin of the predominant plant-type of the present day.

DOUGLAS HOUGHTON CAMPBELL.

STANFORD UNIVERSITY.